Homing and Orientation of Cutthroat Trout (*Salmo clarki*) in Yellowstone Lake, with Special Reference to Olfaction and Vision[1,2]

By James D. McCleave[3]

Department of Zoology and Entomology
Montana State University, Bozeman, Montana

ABSTRACT

In-season homing was exhibited by mature cutthroat trout (*Salmo clarki*) displaced from spawning tributaries to Yellowstone Lake during late May to early August 1964, 1965, and 1966. Of 1908 trout tagged and displaced from Clear and Cub creeks to three release points in the lake (1.55–7.95 km) and to the mouths of the streams, 614 (32.2%) homed, 119 (6.2%) strayed, and 28 (1.5%) were captured by anglers. Only slight differences in homing performance from various release points occurred, but there were differences among years and between streams. Adjusted mean homing times from the various release points ranged from 16 hr to 155 hr, with an inverse relation between homing times and the distance to the release point apparent in one year. Blockage of the olfactory or visual sense did not affect the per cent of trout homing or straying. However, visual clues did increase the speed of homing, since homing times for blinded trout were much longer than for olfactory-occluded, control (anesthetized only), or non-anesthetized trout. A compass-type orientation occurred which was apparently not in response to visual or olfactory stimuli. A general east-northeastward (Clear and Pelican Creek trout) or northward (Cub Creek trout) orientation was exhibited by blind, anosmic, control, and non-anesthetized trout that were float-tracked from an open-water point. Blind and anosmic trout oriented as well as control trout. The directions of orientation were not in the directions of the home-streams, and orientation was not at a constant angle to the current directions or the sun azimuths.

INTRODUCTION

Homing and orientation behavior of mature cutthroat trout (*Salmo clarki*) after displacement from spawning tributaries to Yellowstone Lake was studied during late May to early August 1964, 1965, and 1966. The objectives were to determine in-season homing performance of tagged displaced trout, and the role of olfaction and vision in orientation and homing.

Gerking (1959) used the term *homing* in a general sense to mean the return of fish, after migratory, accidental, or experimental displacement, "to a place formerly occupied instead of going to other equally probable places." He defined equally probable places as areas "occupied by other individuals of the same species" (S. D. Gerking, unpublished). In spawning migrations of fishes, three types of homing are recognized: (1) the return of adults to spawn in the same location in which they were hatched, i.e. "reproductive homing" (Lindsey et al., 1959), or parent stream or natal homing;

[1]Received for publication March 7, 1967.
[2]Contribution from Montana State University Agricultural Experiment Station, Project No. MS844; Paper No. 802, Journal Series.
[3]Present address: Department of Biological Sciences, Western Illinois University, Macomb, Illinois.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

(2) the return of adults to spawn in subsequent breeding seasons at the location of initial spawning, i.e. repeat homing; and (3) the return of adults within the same breeding season to the location of initial choice after displacement, i.e. in-season homing. Horrall (MS, 1961) refers to all three as reproductive homing.

Ball (1955) validated the parent stream homing theory for cutthroat trout in Yellowstone Lake. Of 460 fingerlings marked at age I on their downstream migration from Arnica Creek to the lake, 94 (20%) returned at age III or IV as adults. Nearly all of these must have been recruit spawners, since the majority of Arnica Creek fish spawn initially at ages IV and V with a few at age III or VI (Bulkley, 1961), and the survival for more than one spawning is usually less than 10% (Ball and Cope, 1961). Traps were operated on five other major spawning tributaries during this period, but no stray fish were captured.

Cutthroat trout in Yellowstone Lake also home for repeat spawning. Cope (1957) tagged 18,836 adults as they entered one of five tributaries to spawn. In subsequent years 244 (1.3%) were recaptured as repeat spawners, and only 8 of these were recaptured in tributaries other than the original. Of the recaptures 97% homed.

No in-season homing experiments were done in Yellowstone Lake prior to the present study. However, Platts (1959) conducted such experiments in a high altitude reservoir in Utah. Mature cutthroat trout migrating up tributaries were captured, spawned artificially, tagged, and returned 1.6–6.4 km into the reservoir. Of 2068 such fish, 1096 (53%) reentered tributaries, and 90% of these chose the streams from which they were taken, the rest being recaptured in other tributaries as strays. Apparently the homing motivation was not completely suppressed by stripping of the reproductive products. In-season homing has also been demonstrated in brook trout (Vladykov, 1942), brown trout (Stuart, 1957), charr (Frost, 1963), sockeye salmon (Hartman and Raleigh, 1964), and pink salmon (Helle, 1966).

Griffin (1952) classified migratory behavior into three categories based on the method used in finding the goal. Hasler et al. (1958) modified the classification as follows: Type I — the ability to find home by use of landmarks in familiar territory and search in unfamiliar territory; Type II — the ability to maintain a constant compass direction in the sense of dead reckoning; Type III — the ability to find home by true navigation involving corrective feedback.

Saila and Shappy (1963) and Patten (1964) proposed two mathematical models of salmon migration in which search on the part of the fish could account for the observed returns. Hasler and Wisby (1958) and Hasler (1956a) have evidence that landmarks may be used in familiar territory. Home water odor may be considered a landmark. Bluntnose minnows (*Pimephales notatus*) (Hasler and Wisby, 1951) and juvenile sockeye salmon (McBride et al., 1964) learned to distinguish between two natural waters by olfaction. Migrating adult sockeye salmon showed olfactory recognition of their home waters by

their activity in a tank (Idler et al., 1961; Fagerlund et al., 1963) and chinook salmon (*O. tshawytscha*) by electroencephalographic responses (Hara et al., 1965). Wisby and Hasler (1954) showed that coho salmon use olfaction to choose between tributaries of a river system.

Jahn (1966) showed that Yellowstone Lake cutthroat trout, displaced westward from their upstream spawning migration to a near shore point or a mid-lake point, displayed a general eastward orientation when continuously tracked for up to 2 hr. The orientation mechanism was not determined, but the sun may have been used as a reference. Hasler et al. (1958) first demonstrated the sun compass (Type II) orientation in white bass (*Roccus chrysops*), bluegill (*Lepomis macrochirus*), and pumpkinseed (*L. gibbosus*). Johnson and Groot (1963) and Groot (1965) have shown celestial orientation of young sockeye salmon. Hasler (1956b, 1960a, b, 1966) and Brett and Groot (1963) reviewed the roles of both vision and olfaction in homing.

METHODS AND MATERIALS

Description of Study Area

Yellowstone Lake (Fig. 1) has an area of 354 km^2 and a maximum depth of 98 m (42 m mean), and lies at an elevation of 2358 m just east of the continental divide in southeast Yellowstone National Park, Wyoming. Benson (1961) has given basic limnological information for this lake. The lake is well suited for homing studies since it is large and has enough tributaries (about 35) to provide adequate choice. It has an endemic cutthroat trout population, and has not been stocked with trout from other waters.

Release points A, B, and C (Fig. 1) were established equidistant on a line from the mouth of Pelican Creek to the mouth of Clear Creek. Distances (kilometers) from the release points to the stream mouths are as follows:

	A	B	C
Mouth of Pelican Creek	2.65	5.30	7.95
Mouth of Clear Creek	7.95	5.30	2.65
Mouth of Cub Creek	6.55	4.00	1.55

In 1964 these points were identified by sighting landmarks with unaided eye each time a release was made. In 1965 and 1966 point B was located with the aid of a sextant and a marker buoy was positioned there. In 1965 points A and C were not used, and in 1966 they were located with the aid of a sextant at the time of each release. Points D and E are in the mouths of Clear and Cub creeks respectively, and are 1.65 km from one another.

Homing Studies

Tagging and displacement of 1137 Clear Creek and 771 Cub Creek cutthroat trout were done from July 15 to 27, 1964, July 7 to 17, 1965, and June 27 to July 13, 1966.

The trout used were sexually mature, were moving upstream to spawn, and were collected from fish traps. The Clear Creek trap was about 75 m

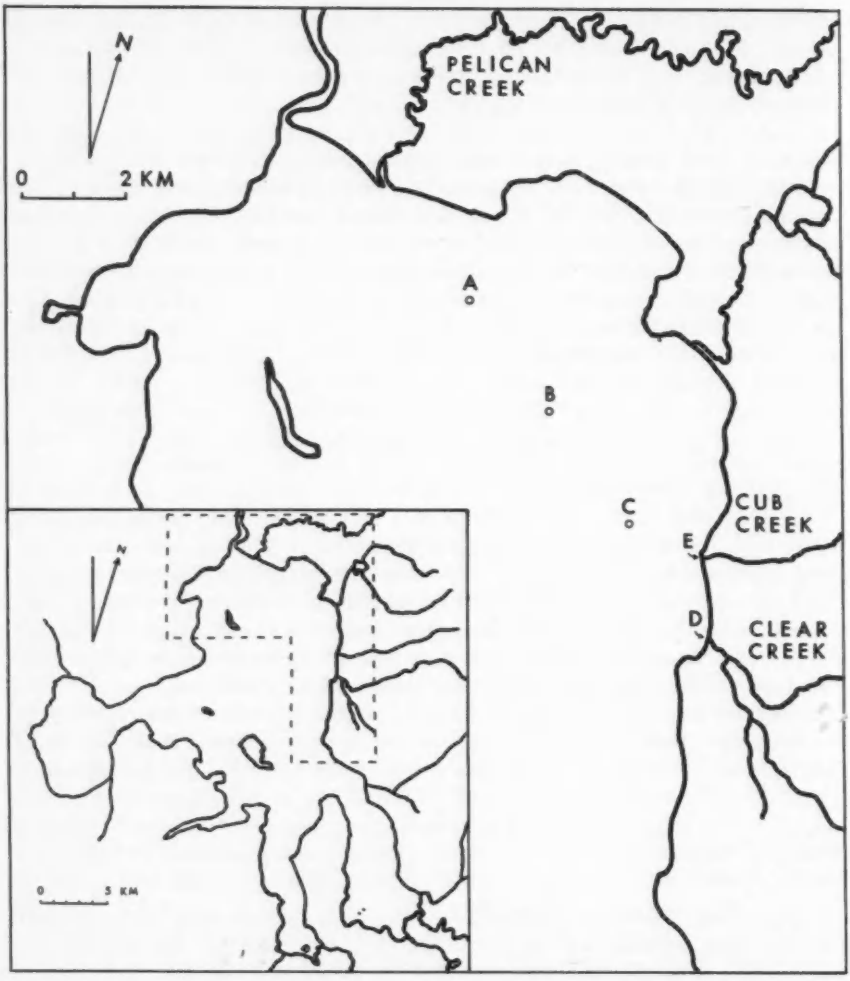

FIG. 1. Northern portion of Yellowstone Lake showing release points and creeks where experimental cutthroat were trapped. Inset shows entire lake and principal tributaries.

above the stream mouth. The Cub Creek trap was about 45 m above the mouth in 1964, but about 150 m above in 1965 and 1966, because the creek shifted its course.

In 1964 a few fish at a time were netted from the trap and immediately placed in 15 liters of 1:5000 tricaine methanesulfonate (M.S. 222, Sandoz Pharmaceuticals) solution. After the fish were anesthetized, a numbered monel strap tag (35.0 mm × 3.5 mm) was attached to the posterior edge of the

operculum with the aid of a special plier. The total length of each fish was recorded. The sex was also recorded if obvious without extra handling. The fish recovered from the anesthetic after being placed in a covered tub containing 20–25 liters of freshwater. After several fish were tagged, the tub was either carried to a boat and the contents emptied into a covered stock tank, or, if the release was to be made at the mouth of the same stream, carried directly to the stream mouth and the fish released. This procedure was repeated until the desired number of fish (10–50) were tagged and either released or placed in the tank. Water was added to make 115–175 liters in the tank. Approximate travel times to release points were as follows (minutes): to point A, 30; point B, 20; point C, 10; and between streams, 8. The maximum time from netting to release was always less than 2 hr, depending on distance to release point and number of fish tagged. Distress of fish at a release point occurred only in two instances. Thirty-nine trout were not anesthetized and were marked by punching a 6.5-mm hole in the dorsal or caudal fin with a paper punch.

In 1965 and 1966, 5–15 fish were netted from the trap, immediately placed in a covered tub containing 20–25 liters of water, and carried either to the stream mouth or to the stock tank in a boat. This was repeated until the desired number of fish were secured. In 1965, 33–50 fish were released in each group, but in 1966 the number was 25. In addition several extra fish were carried along as spares. It took 16–20 min to reach release point A, 10–13 min to B, 6–8 min to C, and 5–7 min from one stream to the other.

In 1965 and 1966 tagging was done at the release point without anesthetizing or measuring the fish. A 28-mm × 5-mm alligator clip (Minigator, Mueller Co.) was attached to the posterior edge of the dorsal fin at its base with the long axis resting on the dorsal midline of the fish (McCleave et al., 1967). Release groups were identified in 1965 by a common color code sprayed onto the clips. In 1966 the clips were individually coded by clamping numbered vinyl tubing (Spaghetti FT-4, Floy Tag and Mfg.) inside the prongs which normally clamp a wire. This did not increase the size of the tag but allowed recognition of each fish. Each fish was released immediately after tagging. The maximum time from netting to release was always less than 40 min. Nearly all fish were hauled under relatively calm lake conditions, but occasionally some sloshing of water did occur in the tank.

The fish traps were operated continuously throughout the spawning season except for brief periods of flood conditions. The traps were emptied by a U.S. Fish and Wildlife Service crew or by me and my colleagues and at least once each day, and two or three times when the run was large. All fish were examined for tags. Code or tag numbers, date, time, total length, and sex were recorded for all recaptured fish. In addition the U.S. Fish and Wildlife Service periodically electrofished in various portions of the lake and outlet throughout all three summers and all captured trout were examined for tags. A number of tags were returned by anglers although their help was not solicited.

During 1966, releases were also made of tagged blinded, olfactory occluded (anosmic), and anesthetized controls, using the same general procedure as with the previously described 1966 releases.

At release point B, 1–5 fish at a time were anesthetized (1.0–1.5 min) in 1:7500 M.S. 222 solution. Fish were blinded by injecting 0.10–0.15 cm^3 of 3% aqueous benzethonium chloride (Phemerol, Parke Davis and Co.) into the eyeball. The eye became opaque and turned green immediately, and after several hours changed to white. Plugging of the nares was done with melted distilled acetylated monoglycerides (Myvacet, Type 5-00, Distillation Products Industries, Eastman Kodak Co.) (Bardach and Case, 1965). The warmed material (which is liquid above 43 C) was injected from a veterinary syringe using a blunt needle into either the anterior or the posterior naris on each side until it began to flow from the other naris. It immediately congealed into a tough, waxy solid which blocked water passage. Each fish was tagged with a numbered alligator clip and placed in a tub containing 25–30 liters of freshwater for a period of 4–7 min, and then released. Time from netting to release was less than 58 min for blind fish, less than 73 min for anosmic fish, and less than 45 min for control fish. Equal numbers of blind and control fish were released on one day, and equal numbers of anosmic and control fish were released on a different day. The heads of all recaptured anosmic fish were preserved for examination of the olfactory plugs.

Float-Tracking Studies

The polystyrene foam (Styrofoam, Dow Chemical Co.) float-tracking method described by Jahn (1966) was used to determine direction of "take-off" of mature, migrating cutthroat trout displaced from tributaries to point B. The floats were Styrofoam cubes 5 cm on a side wrapped with aluminum foil. Each of these was connected by a 2-m nylon thread to an alligator clip used to attach the device to the dorsal fin.

Four experimental groups of trout were tracked: blind (anesthetized and blinded), anosmic (anesthetized and olfactory occluded), control (anesthetized only), and non-anesthetized. Blind, control, and non-anesthetized Cub Creek trout and blind, anosmic, and control Clear Creek trout were tracked in 1965. Blind, anosmic, and control Clear, Cub, and Pelican Creek trout were tracked in 1966. In 1965, 37 Clear Creek and 21 Cub Creek trout and in 1966, 56 Clear Creek, 6 Cub Creek, and 24 Pelican Creek trout were float-tracked beginning at point B.

In 1965, 8–12 trout were netted from the traps and carried in two covered tubs of 20–30 liters water to the boat and either placed in the boat or emptied into a covered stock tank for transportation. Non-anesthetized trout were transported to point B, the floats attached, and 10 individuals released with as little handling as possible. All trout for the olfaction experiment were taken to point B and anesthetized in 1:7500 M.S. 222 solution. The nares of half of these were plugged using cotton soaked in Phemerol. Trout were allowed to recover in freshwater and then floats attached. Five anosmic and five control

trout were released. Trout for the blinding experiments were treated in one of three ways. Most were hauled in tubs or a stock tank just offshore from the collection stream and anesthetized. Half of these were blinded by Phemerol injection and all were allowed to recover during the rest of the trip to point B. On one occasion several Clear Creek trout were hauled to the release point before anesthetizing and blinding. On two other occasions Clear Creek trout were anesthetized at the trap site and half of them were blinded. All were placed in a live-holding box for recovery, one group for 91 hr, the other for 19 hr, before transportation to point B. Either four blind and four control trout or three blind and three control trout were released for each experiment.

In 1966, 4–10 trout were removed from the Clear, Cub, and Pelican Creek traps and carried to the boat. The Pelican Creek trap, about 2 km upstream from the mouth, was not very effective because of flood damage, but enough trout were captured for float-tracking experiments. Pelican Creek trout were transported in 35–40 liters of water by truck 4.4 km (about 5 min) to the boat, and Clear and Cub Creek trout were transported as in 1965. Just offshore the trout were anesthetized. Some were blinded with Phemerol, some plugged with either white petroleum jelly injected through a needleless syringe or with warmed Myvacet, and some simply placed back in freshwater. All were allowed to recover on the remainder of the trip to point B. Usually six trout (two blind, two anosmic, two control) were released at a time, but on one occasion only one of each kind was released. With the exception of those blind trout held in the live box, the time from netting to release was always no more than 90 min and usually less than 70 min.

Trout with attached floats were released individually, and sufficient time was allowed between releases to avoid entanglement of the floats. In all but the initial five 1965 experiments, a drift drogue (Jahn, 1966) suspended at 1 m was released as soon as the last fish had cleared the release area. After experimental fish had been at large for an average of 1 hr, a large, stable azimuth sighting compass was used to obtain a bearing (to the nearest degree) from each fish to the release buoy. Distance to the buoy was not measured. After each sighting an attempt was made to pick up the trout for length measurement, sex determination, and in 1966 also for tagging with a numbered alligator clip. Nearly all fish were picked up, but a few pulled loose from the float or were not found before the termination of the experiment. A bearing from the drogue to the buoy was taken and the drogue recovered.

In 1965 one control and one blind trout and in 1966 one non-anesthetized trout (all from Clear Creek) were float-tracked individually from Point B for longer periods (3 hr, 26 min–6 hr, 20 min). These fish were subjected to the same treatment as groups in the short term experiments described previously. Sextant sightings of landmarks were used to make position plots at 15–45-min intervals depending on how far the fish moved. All experiments were terminated when the lake surface became so rough that accurate position plots were impossible.

Statistical Analyses

Homing Studies.— Chi-square analyses were used to compare the numbers of trout recaptured from various releases. The expected number of fish in each cell of the chi-square computation formula was obtained by multiplying the per cent recapture of all release groups in the comparison by the number of fish in the release group.

The times from release to recapture for various release groups were compared using an analysis of variance for unequal sample sizes (Steel and Torrie, 1960). Since the distribution of time to recapture (in hours) was skewed toward the longer times, each time value was transformed to its square root. All statistical analyses were performed on transformed data, but the mean time values are presented in hours. The adjusted mean is the square of the mean of the transformed data. If the analyses of variance did not yield significant F values, Bartlett's test for homogeneity of variance (Bartlett, 1937a, b) was done as a further check on the assumptions of the analysis of variance model. If more than two release groups were compared in any analysis of variance, Duncan's new multiple-range test (Duncan, 1955) was performed on the ranked means of the transformed data to compare all pairs of means.

Float-Tracking Studies.— The observed directions from the release buoy to float-tracked trout were represented as points of equal mass on the circumference of a circle. An empirical mean vector pointing to the center of mass of the distribution of each group of fish was calculated with polar coordinates r (length) and a (angle) (Batschelet, 1965). The Rayleigh test (Greenwood and Durand, 1955) for a significant r value was then used. If r was significantly greater than zero, the null hypothesis of a uniform circular distribution was rejected. A resultant vector F test (Watson and Williams, 1956) was used to compare the mean directions (a) of two groups of tracked trout. Another test statistic, R, based on a resultant vector (Watson and Williams, 1956; Stephens, 1962), was used to determine if the mean direction (a) of a group of trout was significantly different from the homestream direction. A concise discussion of all these methods is given by Batschelet (1965).

RESULTS

Homing Studies

Clear Creek trout homed equally well in 1965 and 1966 and better ($P < 0.01$) in both years than in 1964 (Tables I, II). The same was true of Cub Creek trout.The percentage of trout homing was greater than the percentage straying in all 3 years for each stream. Straying of both Clear and Cub Creek trout was greater in 1966 than in 1964, and of Clear Creek trout in 1965 than in 1964. Straying was about equal among Cub Creek trout in 1965 and 1966, but among Clear Creek trout it was greater in 1966 than in 1965. Total recapture percentages (including angler returns) for each stream were about equal in 1965 and 1966, and were greater than in 1964.

In 1964 the per cent of trout that homed was greater for Cub than for Clear Creek trout, but in 1965 and 1966 the reverse was true. In all three

TABLE I. Summary of displacement and recapture of Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966. (Percentages in parentheses.)

Year	Release point	No. released	No. of recaptures: Homing	Straying	Angling	Total
		Clear Creek				
1964	A	35	4(11.4)[a]	1(2.9)	1(2.9)	6(17.1)
	B	150	7(4.7)	1(0.7)	2(1.3)	10(6.7)
	C	158	18(11.4)[b]	2(1.3)	3(1.9)[c]	23(14.6)
	Mouth Clear Creek	20	3(15.0)	0(0.0)	1(5.0)	4(20.0)
	Total	363	32(8.8)	4(1.1)	7(1.9)	43(11.8)
1965	B	274	122(44.5)	7(2.6)	2(0.7)	131(47.8)
	Inside Mouth Clear Creek	50	24(48.0)	0(0.0)	0(0.0)	24(48.0)
	Ouside Mouth Clear Creek	50	24(48.0)	0(0.0)	0(0.0)	24(48.0)
	Total	374	170(45.5)	7(1.9)	2(0.5)	179(47.9)
1966	A	100	45(45.0)	2(2.0)	3(3.0)[d]	50(50.0)
	B	100	43(43.0)	5(5.0)	1(1.0)	49(49.0)
	C	100	42(42.0)	5(5.0)	1(1.0)	48(48.0)
	Mouth Clear Creek	50	24(48.0)	3(6.0)	0(0.0)	27(54.0)
	Mouth Cub Creek	50	20(40.0)	3(6.0)	1(2.0)	24(48.0)
	Total	400	174(43.5)	18(4.5)	6(1.5)	198(49.5)
	Clear Creek all years combined	1137	376(33.1)	29(2.6)	15(1.3)	420(36.9)
		Cub Creek				
1964	B	20	4(20.0)	0(0.0)	1(5.0)	5(25.0)
	C	106	19(17.9)	5(4.7)	3(2.8)	27(25.5)
	Mouth Cub Creek	10	1(10.0)	1(10.0)	0(0.0)	2(20.0)
	Mouth Clear Creek	10	4(40.0)	1(10.0)	1(10.0)[c]	6(60.0)
	Total	146	28(19.2)	7(4.8)	5(3.4)	40(27.4)
1965	B	175	57(32.6)	27(15.4)	1(0.6)	85(48.6)
	Inside Mouth Cub Creek	25	9(36.0)	0(0.0)	0(0.0)	9(36.0)
	Outside Mouth Cub Creek	25	9(36.0)	2(8.0)	0(0.0)	11(44.0)
	Total	225	75(33.3)	29(12.9)	1(0.4)	105(46.7)
1966	A	100	30(30.0)	12(12.0)	1(1.0)	43(43.0)
	B	100	27(27.0)	9(9.0)	2(2.0)	38(38.0)
	C	100	34(34.0)	20(20.0)	2(2.0)	56(56.0)
	Mouth Clear Creek	50	17(34.0)	11(22.0)	1(2.0)	29(58.0)
	Mouth Cub Creek	50	27(54.0)	2(4.0)	1(2.0)	30(60.0)
	Total	400	135(33.8)	54(13.5)	7(1.8)	196(49.0)
	Cub Creek all years combined	771	238(30.9)	90(11.7)	13(1.7)	341(44.2)
	Grand total	1908	614(32.2)	119(6.2)	28(1.5)	761(39.0)

[a]Includes one fish recaptured in 1966.
[b]Includes one fish recaptured in 1965 and another in 1966.
[c]Includes one fish recaptured in home stream previously.
[d]Includes one fish recaptured by electrofishing.

TABLE II. Chi-square comparisons of the recaptures of Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966.

Origin stream	Year	Release point(s)	Recapture category	vs. Origin stream	Year	Release point(s)	Recapture category	Chi-square[a]
Clear	1964	Combined	Home	Clear	1965	Combined	Home	90.24**
	1964				1966			84.78**
	1965				1966			0.17
	1964		Stray		1965		Stray	0.74
	1964				1966			7.62**
	1965				1966			4.14*
	1964		Total		1965		Total	79.33**
	1964				1966			85.41**
	1965				1966			0.11
Cub	1964	Combined	Home	Cub	1965	Combined	Home	6.39*
	1964				1966			7.61**
	1965				1966			0.01
	1964		Stray		1965		Stray	5.97*
	1964				1966			7.36**
	1965				1966			0.04
	1964		Total		1965		Total	8.41**
	1964				1966			11.55**
	1965				1966			0.16
Clear	1964	Combined	Home	Clear	1964	Combined	Stray	21.80**
	1965				1965			150.10**
	1966				1966			126.76**
Cub	1964	Combined	Home	Cub	1964	Combined	Stray	12.60**
	1965				1965			20.34**
	1966				1966			34.72**
Clear	1964	Combined	Home	Cub	1964	Combined	Home	9.48**
			Stray				Stray	6.56*
			Total				Total	15.45**
Clear	1965	Combined	Home	Cub	1965	Combined	Home	5.05*
			Stray				Stray	28.38**
			Total				Total	0.04

Clear	1966	Combined	Home	Cub	1966	Combined	Home	4.92*
			Stray				Stray	18.00**
			Total				Total	0.01
Clear	1966	A	Home	Clear	1966	B	Home	0.05
		A				C		0.10
		A				Mouth Clear		0.07
		A				Mouth Cub		0.19
		B				C		0.01
		B				Mouth Clear		0.19
		B				Mouth Cub		0.07
		C				Mouth Clear		0.27
		C				Mouth Cub		0.03
		Mouth Clear				Mouth Cub		0.36
Cub	1966	A	Home	Cub	1966	B	Home	0.16
		A				C		0.25
		A				Mouth Cub		5.05*
		A				Mouth Clear		0.17
		B				C		0.80
		B				Mouth Cub		6.75**
		B				Mouth Clear		0.56
		C				Mouth Cub		3.35
		C				Mouth Clear		0.00
		Mouth Cub				Mouth Clear		2.27
Clear	1964	Mouth Clear	Home	Clear	1964	Open-water points	Home	0.92
	1965				1965			0.19
	1966				1966			0.23
	Combined				Combined			7.94**
Cub	1964	Mouth Cub	Home	Cub	1964	Open-water points	Home	4.47*
	1965				1965			3.26
	1966				1966			7.10**
	Combined				Combined			5.45*

[a]*Significant at $P = 0.05$; **significant at $P = 0.01$.

years Cub Creek trout strayed more than Clear Creek trout. In 1964 the total per cent recapture of Cub Creek trout was greater than that of Clear Creek trout, but in 1965 and 1966 total recaptures for the two streams were about equal.

In 1966, when trout from both creeks were displaced to all release points, no trends in homing were evident among releases at open-water points for trout from either stream. Trout displaced to the mouth of the opposite stream and to open-water homed about equally well. Homing from the mouths of the origin streams tended to be greater than from the other release points.

For the 3 years combined, the percentage homing to Clear Creek from the mouth of Clear Creek was greater than from all open-water points combined. The percentage homing to Cub Creek from the mouth of Cub Creek was less than from the combined open-water points in 1964, about equal to that from open-water points in 1965, and greater in 1966. In 1965, when Clear and Cub Creek trout were released 5–10 m outside or inside the origin stream mouth, homing performance was the same from inside and outside the mouth.

There was no significant difference between the recaptures of males and females in any category (Table III).

In 1964, when 47 opercle-tagged trout and 39 fin-punched trout were displaced from Cub Creek to point C, 6 (13%) of the tagged trout and 8 (21%) of the punched trout homed. One (2%) of the tagged trout and 3 (8%) of the punched trout strayed.

TABLE III. Displacement and recapture of trout of known sex from Clear and Cub creeks, July 15–27, 1964.

		Clear Creek		Cub Creek		Combined	
		♂	♀	♂	♀	♂	♀
No. released		120	107	27	37	147	144
Homing:	No.	14[a]	10	3	6	17	16
	Per cent	11.7	9.3	11.1	16.2	11.6	11.1
	Chi-square	0.48		0.29		0.13	
Straying:	No.	2	0	0	2	2	2
	Per cent	1.7	0.0	0.0	5.4	1.4	1.4
	Chi-square	1.96		1.46		0.00	
Angling:	No.	5[a]	1	2	2	7	3
	Per cent	4.2	0.9	7.4	5.4	4.8	2.1
	Chi-square	2.48		1.00		1.52	
Total:	No.	21[a]	11	5	10	26	21
	Per cent	17.5	10.3	18.5	27.0	17.7	14.6
	Chi-square	2.50		0.48		0.43	

[a]Includes one fish counted as both homing and angling.

In 1964 no trends in homing times were evident among Clear and Cub Creek trout displaced to the various open-water release points, but homing time from the mouths of the origin streams was less than from openwater points (Tables IV, V). In 1965 Clear Creek trout released 5–10 m inside the mouth of Clear Creek homed faster than those released either 5–10 m outside the mouth or at point B. Little difference in homing times was found in 1965 Cub Creek trout. In 1966 a pattern in adjusted mean homing times was exhibited by both Clear and Cub Creek trout. Homing times were inversely related to distance for all points (except the opposite stream mouth): trout released at the farthest point (A) homed the fastest and those at the mouth of the origin stream the slowest. Those trout released at the mouths of the opposite streams homed in about equal time to those from the mouths of the origin streams.

There were no differences in the mean homing times between Clear and Cub Creek trout from open-water points in 1964, 1965, and 1966, except that in 1964 Cub Creek trout homed faster than Clear Creek trout from point C (Tables IV, VI). Cub Creek trout did not home consistently faster than Clear Creek trout even though Cub Creek is nearer to the open-water release points.

Clear and Cub Creek trout homed faster from point B in 1965 than in 1966 (Tables IV, VII). Homing times in 1964 were not compared statistically with those in 1965 and 1966 due to different tagging procedures, but in 1964 homing times were considerably less than in 1965 and 1966.

In 1965 and 1966, when sample sizes were largest, homing times from open-water points were usually not significantly different for males and females from both Clear and Cub creeks (Tables VIII, IX).

The results of experiments involving 50 blind, 50 anosmic, and two groups (A and B) of 50 control (anesthetized only) trout displaced from Clear Creek to point B in 1966 are given in Table X. The performance of two groups (A and B) of 25 non-anesthetized trout already included in other experiments are used for comparison with the blind, anosmic, and control groups, which were all anesthetized before tagging.

There was little difference in the percentages of trout homing among the release groups. The anosmic, control B, and non-anesthetized B groups tended to stray more than the three groups released 7–9 days earlier. The total recapture percentages of all groups were not different. Thus blind trout were able to home as well as control trout, and anesthetization per se affected homing performance only slightly if at all. Thirty anosmic trout were recaptured, but 22 had lost one or both nasal plugs. Of these, 16 homed and 6 strayed. Of the 8 whose plugs were intact, 7 homed, 1 strayed.

Mean homing times of the one blind, one anosmic, two control, and two non-anesthetized groups of trout were not equal (Tables XI, XII). The blind, control A, and non-anesthetized A groups all homed more slowly than the anosmic, control B, and non-anesthetized B groups, which were released at a later time. The blind trout were also slower than the control A and non-anesthetized A groups. The anosmic group homed in about the same length

TABLE IV. Times (hours) from release to recapture of displaced Clear and Cub Creek trout during late June and July, 1964, 1965, and 1966.[a]

Year	Release point	Homing time				Straying time			
		Mean	Adjusted mean	Range	Sample size	Mean	Adjusted mean	Range	Sample size
				Clear Creek					
1964	A	116.7	111.8	69–184	3	58.0	58.0	58	1
	B	57.9	53.9	15–104	7	121.0	121.0	121	1
	C	69.7	65.0	25–142	16	32.0	30.8	20–44	2
	Mouth Clear	35.0	16.4	1–103	3				0
1965	B	99.1	91.7	8–432	118	118.1	112.0	55–200	7
	Mouth Clear (in)	60.7	45.7	5–409	24				0
	Mouth Clear (out)	121.2	105.8	6–599	21				0
1966	A	103.3	96.0	12–272	45	33.0	33.0	33	2
	B	126.8	113.6	8–297	42	134.5	122.1	33–243	4
	C	126.6	118.2	31–308	42	58.4	49.7	6–127	5
	Mouth Clear	164.5	154.7	27–268	23	115.0	99.7	28–221	3
	Mouth Cub	158.6	150.2	73–337	18	162.3	158.0	93–201	3
				Cub Creek					
1964	B	52.3	51.6	34–59	4				0
	C	42.3	40.5	23–71	10	49.0	45.3	23–75	2
	Mouth Cub	34.0	34.0	34	1	34.0	34.0	34	1
	Mouth Clear	70.8	70.5	58–75	4	32.0	32.0	32	1
1965	B	86.2	82.0	34–198	56	109.0	94.3	10–343	25
	Mouth Cub (in)	90.6	85.2	32–152	9				0
	Mouth Cub (out)	71.2	67.1	32–151	9	39.5	38.8	29–50	2
1966	A	108.9	101.6	31–296	29	100.5	90.9	33–200	12
	B	122.6	111.0	26–363	27	107.4	101.1	32–174	8
	C	139.6	127.4	30–462	34	98.1	84.5	6–241	20
	Mouth Clear	146.8	138.5	30–296	18	71.0	50.6	3–196	10
	Mouth Cub	136.8	132.3	58–272	27	126.5	125.3	102–151	2

[a]Significant comparisons by Duncan's new multiple-range test: Clear Creek trout — 1964 A, C ($P<0.01$); 1964 C, Mouth Clear Creek ($P<0.05$); 1965 B, Mouth Clear Creek (in) ($P<0.01$); 1965 Mouth Clear Creek (in), Mouth Clear Creek (out) ($P<0.01$); 1966 A, Mouth Clear Creek ($P< 0.05$); Cub Creek trout — 1964 C, Mouth Clear Creek ($P<0.05$).

TABLE V. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing times of Clear and Cub Creek trout from various release points in 1964, 1965, and 1966.

	Source of variation	df	Mean square[a]	Bartlett's test: Chi-square
	Clear Creek			
1964	Between release points	3	22.69*	–
	Within release points	25	6.89	
	Total	28		
1965	Between release points	2	91.91**	–
	Within release points	160	9.78	
	Total	162		
1966	Between release points	4	36.21**	–
	Within release points	165	9.76	
	Total	169		
	Cub Creek			
1964	Between release points	3	4.42	3.47
	Within release points	15	1.40	
	Total	18		
1965	Between release points	2	3.21	0.29
	Within release points	71	4.56	
	Total	73		
1966	Between release points	4	12.71	8.09
	Within release points	130	9.33	
	Total	134		

[a]*Significant at $P = 0.05$; **significant at $P = 0.01$.

of time as the control B and non-anesthetized B groups. The homing times of non-anesthetized groups were not different from comparable control groups, so anesthetization per se had no effect on the homing time. The mean homing time of the 7 trout with nasal plugs intact was not significantly greater than that of 16 trout with one or both plugs missing (Tables XI, XII).

FLOAT-TRACKING STUDIES

An eastward or east-northeastward orientation prevailed among blind, anosmic, and control (anesthetized only) trout from Clear Creek in 1965 and 1966 and from Pelican Creek in 1966 (Fig. 2, 3). The only exception was the 1965 anosmic Clear Creek group (4 fish), whose mean direction was south-southeast. Cub Creek trout moved generally northward in 1965; however, in 1966 only two trout in each category were tracked and movements were variable.

Vector lengths (r) were usually greater for Clear and Cub Creek groups in 1965 than in 1966. The r values were greater than zero for blind, control, and combined Clear Creek trout in 1965, blind and combined Cub Creek trout in 1965, anosmic and combined Clear Creek trout in 1966, and control and com-

TABLE VI. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing times between Clear and Cub Creek trout from open-water points in 1964, 1965, and 1966.

	Source of variation	df	Mean square[a]	Bartlett's test: Chi-square
1964	Point B releases			
	Between creeks	1	0.07	2.26
	Within creeks	9	3.31	
	Total	10		
1964	Point C releases			
	Between creeks	1	17.75*	–
	Within creeks	24	3.84	
	Total	25		
1965	Point B releases			
	Between creeks	1	10.30	5.22*
	Within creeks	172	6.50	
	Total	173		
1966	Point A releases			
	Between creeks	1	1.40	0.00
	Within creeks	72	7.51	
	Total	73		
1966	Point B releases			
	Between creeks	1	0.27	0.13
	Within creeks	67	12.99	
	Total	68		
1966	Point C releases			
	Between creeks	1	3.22	1.39
	Within creeks	74	10.33	
	Total	75		

[a]*Significant at $P = 0.05$.

TABLE VII. Analysis of variance of the mean homing times between 1965 and 1966 Clear and Cub Creek trout displaced to Point B.

Source of variation	df	Mean square[a]
Clear Creek		
Between years	1	36.33*
Within years	158	9.08
Total	159	
Cub Creek		
Between years	1	40.05*
Within years	81	6.84
Total	82	

[a]*Significant at $P = 0.05$.

TABLE VIII. Times (hours) from release to recapture in the homestream of male and female trout displaced from Clear and Cub creeks to open-water points during 1965 and 1966.

Year	Release point	Sex	Mean	Adjusted mean	Range	Sample size
			Clear Creek			
1965	B	♂	100.9	95.3	8–202	32
		♀	103.3	93.8	8–366	81
1966	A	♂	108.0	102.9	34–224	17
		♀	103.8	96.6	34–272	27
	B	♂	111.9	97.8	8–223	16
		♀	133.4	121.0	32–297	25
	C	♂	105.0	100.5	50–191	11
		♀	131.3	121.7	31–308	29
			Cub Creek			
1965	B	♂	90.1	87.8	54–177	15
		♀	84.9	79.8	34–198	40
1966	A	♂	124.9	116.7	32–199	7
		♀	103.8	97.0	32–296	22
	B	♂	166.2	159.3	79–294	5
		♀	112.7	101.2	26–363	22
	C	♂	149.8	148.2	102–174	5
		♀	137.9	124.0	30–462	29

bined Pelican Creek trout in 1966 (Table XIV). Since the r values of the combined trout from each stream each year (except Cub Creek trout in 1966) were greater than zero, the non-significance of individual groups may be due to small sample sizes rather than lack of orientation. The r values for Pelican Creek trout were similar to those for 1965 Clear Creek trout.

Blind and anosmic trout oriented at least as well as control trout. Vector lengths for all experimental groups ranged from 0.1919 to 0.9799. Differences among groups from any one stream showed no pattern.

The orientation directions were not the same as the homestream directions for Clear, Cub, or Pelican Creek trout, and were different (R test) from the homestream directions for the following groups: blind, control, and combined Clear Creek trout in 1965; control and combined Cub Creek trout in 1965; anosmic and combined Clear Creek trout in 1966; and anosmic, control, and combined Pelican Creek trout in 1966 (Table XIV).

Differences in mean directions of various groups from the same stream in the same year were slight except between blind and non-anesthetized trout from Cub Creek in 1965 (Table XV). The north orientation of Cub Creek trout in 1965 was different from the east-northeast orientation of Clear Creek trout in 1965. The mean directions of Clear and Cub Creek trout in 1965 were not different from those of 1966.

Within a given group of trout, the r values were usually similar for males and females, and the directions of orientation of males and females were not different (Table XVI).

TABLE IX. Analysis of variance and Bartlett's test of homogeniety of variance of the mean homing times of male and female Clear and Cub Creek trout displaced to open-water points during late June and July, 1965 and 1966.

	Source of variation	df	Mean square	Bartlett's test: Chi-square[a]
		Clear Creek		
1965	Point B			
	Between sexes	1	0.14	2.65
	Within sexes	111	8.51	
	Total	112		
1966	Point A			
	Between sexes	1	1.01	0.40
	Within sexes	42	6.67	
	Total	43		
1966	Point B			
	Between sexes	1	12.04	0.05
	Within sexes	39	13.68	
	Total	40		
1966	Point C			
	Between sexes	1	8.12	1.80
	Within sexes	38	8.62	
	Total	39		
		Cub Creek		
1965	Point B			
	Between sexes	1	2.07	2.47
	Within sexes	53	4.46	
	Total	54		
1966	Point A			
	Between sexes	1	4.82	0.20
	Within sexes	27	7.65	
	Total	28		
1966	Point B			
	Between sexes	1	26.72	0.65
	Within sexes	25	11.54	
	Total	26		
1966	Point C			
	Between sexes	1	4.60	3.88*
	Within sexes	32	12.84	
	Total	33		

[a]*Significant at $P = 0.05$.

Since the water current directions during the float-tracking experiments appeared to be clustered (Fig. 2, 3), the following analysis was done to determine if trout orientation was related to drift with the current or movement at some constant angle to the current. The current direction (in degrees from

TABLE X. Recaptures of blind, anosmic, control (anesthetized only), and non-anesthetized trout displaced from Clear Creek to point B, 1966. (Percentages in parentheses.)

Release date	Experimental group	No. released	No. of recaptures		
			Homing	Straying	Total
July 4	Non-anesthetized A	25	14(56)	1(4)	15(60)
5	Control A	50	25(50)	2(4)	27(54)
5	Blind	50	25(50)	3(6)	28(56)
12	Anosmic	50	23(46)	7(14)	30(60)
12	Control B	50	16(32)	5(10)	21(42)
13	Non-anesthetized B	25	13(52)	2(8)	15(60)
Chi-square			3.18	4.25	2.01

TABLE XI. Times (hours) from release to recapture in the homestream of blind, anosmic, control (anesthetized only), and non-anesthetized Clear Creek trout displaced to point B, 1966.

Release date	Experimental group	Time			Sample size
		Mean	Adjusted mean	Range	
July 4	Non-anesthetized A	148.2	139.8	34–271	14
5	Control A	114.7	108.7	10–200	25
5	Blind	237.8	222.3	78–479	25
12	Anosmic	63.5	58.4	27–174	23
12	Control B	66.6	63.4	27–126	16
13	Non-anesthetized B	60.7	52.7	8–126	12
Anosmic	Plugs intact	74.6	71.6	30–125	7
Anosmic	1–2 plugs lost	58.8	53.1	27–174	16

TABLE XII. Analysis of variance and Bartlett's test of homogeneity of variance of the mean homing times of blind, anosmic, control (anesthetized only), and non-anesthetized trout from Clear Creek displaced to point B, 1966.

Source of variation	df	Mean square[a]	Bartlett's test: Chi-square
All groups analysis			
Between groups	5	184.91**	–
Within groups	109	8.44	
Total	114		
Anosmic group: intact vs. lost plugs			
Between groups	1	6.77	0.63
Within groups	21	5.32	
Total	22		

[a]**Significant at $P = 0.01$.

TABLE XIII. Duncan's new multiple-range comparisons of the mean homing times of blind, anosmic, control (anesthetized only), and non-anesthetized trout from Clear Creek displaced to point B, 1966.

Comparison between		Difference between means[a]
Blind	Non-anesthetized A	3.08**
Blind	Control A	4.49**
Blind	Control B	6.94**
Blind	Anosmic	7.27**
Blind	Non-anesthetized B	7.65**
Non-anesthetized A	Control A	1.40
Non-anesthetized A	Control B	3.86**
Non-anesthetized A	Anosmic	4.18**
Non-anesthetized A	Non-anesthetized B	4.56**
Control A	Control B	2.45**
Control A	Anosmic	2.78**
Control A	Non-anesthetized B	3.16**
Control B	Anosmic	0.32
Control B	Non-anesthetized B	0.70
Anosmic	Non-anesthetized B	0.38

[a]**Significant at $P = 0.01$.

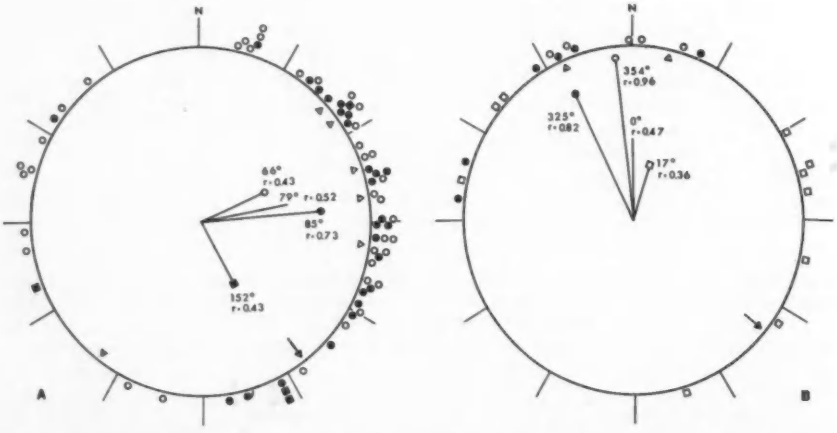

FIG. 2. Directions of "take-off" (plotted in 2° intervals on odd-numbered degrees), mean directions, and vector lengths of (A) blind, anosmic, and control (anesthetized only) Clear Creek trout, and (B) blind, control, and non-anesthetized Cub Creek trout tracked at point B, July 10–29, 1965. Closed circles = blind trout; closed squares = anosmic trout; open circles = control trout; open squares = non-anesthetized trout; open triangles = 1-m current drogue. Arrow points toward homestream. Mean vector of each group identified by appropriate symbol at end of vector. Vector without symbol is combined mean vector.

true North) during each track was subtracted from the direction (in degrees from true North) of each fish in that track. These converted data were then used to calculate the mean directions and vector lengths based on current

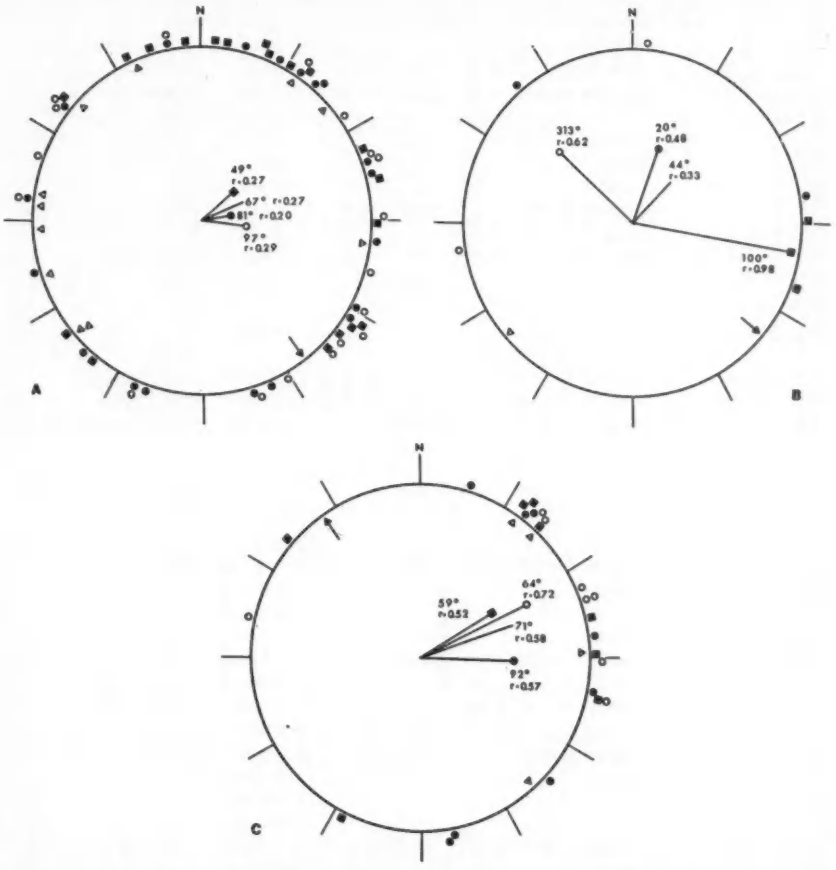

FIG. 3. Directions of "take-off" (plotted in 2° intervals on odd-numbered degrees), mean directions, and vector lengths of blind, anosmic, and control (anesthetized only) trout from (A) Clear Creek, (B) Cub Creek, and (C) Pelican Creek tracked at point B June 2–July 18, 1966. Legend as in Fig. 2.

direction as the zero direction. In general, converted r values were equal to or smaller than unconverted values (Table XVII), but if the trout oriented at a constant angle to the current direction, converted r values would have been greater. Converted angles were in general no more clustered than unconverted angles, but would have been if the trout oriented to the current. The fact that converted r values and a concentrations remained about the same showed that the currents were clustered and not that the trout oriented to the current. In addition Clear Creek trout showed the same east-northeast orientation, but not as strongly, in 1966 when the currents were clustered to the west as in 1965 when they were clustered to the east (Fig. 2, 3). However, in 1965,

TABLE XIV. Tracking times, mean directions (from true North), vector lengths, Rayleigh tests, and homestream tests of blind, anosmic, control (anesthetized only), and non-anesthetized trout from Clear, Cub, and Pelican creeks tracked from point B, 1965, and 1966.

Year	Category	No. tracked	Tracking time (*minutes*)	Mean direction (*a*)	Vector length (*r*)	Rayleigh test[b] (*z*)	Homestream test[b] (R)
			Clear Creek				
1965	Blind	26	86(54–162)[a]	85°	0.7319	13.93**	19.03**
	Anosmic	4	95(55–141)	152	0.4261	–[c]	1.70
	Control	37	79(51–119)	66	0.4332	6.91**	15.99**
	Combined	67	82(51–162)	79	0.5224	18.28**	35.00**
1966	Blind	19	69(53–112)	81	0.1919	0.70	3.65
	Anosmic	19	76(57–104)	49	0.4070	3.15*	7.73*
	Control	18	75(54–94)	97	0.2853	1.47	5.14
	Combined	56	73(53–112)	67	0.2671	3.99*	14.95**
			Cub Creek				
1965	Blind	6	74(56–98)	325	0.8234	4.07*	4.94
	Control	5	64(51–77)	354	0.9615	–[c]	4.81**
	Non-anesthetized	10	85(62–120)	17	0.3562	1.27	3.56
	Combined	21	77(51–120)	0	0.4696	4.63**	9.86*
1966	Blind	2	69(56–81)	20	0.4472	–[c]	–[c]
	Anosmic	2	85(67–102)	100	0.9799	–[c]	–[c]
	Control	2	78(71–84)	313	0.6157	–[c]	–[c]
	Combined	6	77(56–102)	44	0.3262	0.62	1.96
			Pelican Creek				
1966	Blind	8	80(72–89)	92	0.5722	2.62	4.58
	Anosmic	8	74(56–96)	59	0.5197	2.16	4.16*
	Control	8	67(47–94)	64	0.7174	4.12*	5.74*
	Combined	24	74(47–96)	71	0.5847	8.21**	14.03**
Grand total		174	77(47–162)	66	0.3958	27.25**	

[a]Mean; range in parentheses.
[b]*Significant at $P = 0.05$; **significant at $P = 0.01$.
[c]Sample too small for test.

TABLE XV. F-test comparisons of mean directions of float-tracked trout between various groups within streams, between streams, and between years.

Origin stream	Year	Category	vs.	Origin stream	Year	Category	Directions test (F)[a]
Clear	1965	Blind		Clear	1965	Control	1.04
		Anosmic				Control	2.51
		Anosmic				Blind	2.96
Clear	1966	Blind		Clear	1966	Control	<1
		Anosmic				Control	2.07
		Anosmic				Blind	<1
Cub	1965	Blind		Cub	1965	Control	2.22
		Blind				Non-anesthetized	6.33*
		Control				Non-anesthetized	3.68
Cub	1966	Blind		Cub	1966	Control	<1
		Anosmic				Control	5.04
		Anosmic				Blind	1.09
Pelican	1966	Blind		Pelican	1966	Control	<1
		Anosmic				Control	<1
		Anosmic				Blind	<1
Clear	1965	Blind		Cub	1965	Blind	25.71**
		Control				Control	5.21*
		Combined[b]				Combined[c]	13.40**
Clear	1966	Blind		Cub	1966	Blind	<1
		Anosmic				Anosmic	1.29
		Control				Control	2.86
		Combined				Combined	<1
Clear	1966	Blind		Pelican	1966	Blind	<1
		Anosmic				Anosmic	<1
		Control				Control	<1
		Combined				Combined	<1
Pelican	1966	Blind		Cub	1966	Blind	1.05
		Anosmic				Anosmic	<1
		Control				Control	4.08
		Combined				Combined	<1
Clear	1965	Blind		Clear	1966	Blind	<1
		Anosmic				Anosmic	3.30
		Control				Control	<1
		Combined				Combined	<1
Cub	1965	Blind		Cub	1966	Blind	<1
		Control				Control	1.25
		Combined[c]				Combined[b]	<1

[a]*Significant at $P = 0.05$; **significant at $P = 0.01$.
[b]Includes anosmic trout.
[c]Includes non-anesthetized trout.

Cub Creek trout oriented toward the north, and the currents moved northward. Trout moved much farther than the current drogue drifted during the tracking period.

Since most of the float-tracking was done during the morning, the sun azimuths during the experiments were highly clustered. The average sun

TABLE XVI. Mean directions, vector lengths, and directions test comparisons of male and female trout float-tracked at point B, 1965 and 1966.

Year	Category	Sex	No. tracked	Mean direction (a)	Vector length (r)	Directions test (F)
			Clear Creek			
1965	Blind	♂	3	61°	0.7940	<1
		♀	18	82	0.8152	
	Control	♂	8	46	0.5221	<1
		♀	13	85	0.4066	
	Combined	♂	11	51	0.5907	3.52
		♀	31	95	0.6404	
1966	Blind	♂	9	336	0.1423	2.27
		♀	10	98	0.4173	
	Anosmic	♂	8	56	0.3678	<1
		♀	9	12	0.4870	
	Control	♂	8	121	0.4803	1.40
		♀	9	60	0.3487	
	Combined	♂	25	81	0.2113	<1
		♀	28	56	0.3349	
			Pelican Creek			
1966	Blind	♂	1	101	1.0000	1.96
		♀	3	46	0.8879	
	Anosmic	♂	2	98	0.7431	2.23
		♀	4	94	0.5456	
	Control	♂	3	70	0.9125	<1
		♀	5	58	0.6075	
	Combined	♂	6	57	0.6683	<1
		♀	12	63	0.6193	

azimuth during the time at large of each trout was subtracted from the direction from point B to the trout. Mean vectors were calculated from these converted data for comparison with unconverted data. Converted vector lengths were usually the same or slightly smaller than unconverted vector lengths, and converted angles were no more clustered than unconverted angles (Table XVIII). Thus the trout probably did not orient at a constant angle to the sun azimuth. No tracks were made when the sun was completely obscured.

At the termination of each float-tracking experiment in 1966 most of the trout were tagged and released near point B. Percentage recaptures of float-tracked trout from Clear and Cub creeks (Table XIX) were slightly lower than those of tagged displaced trout from Clear and Cub creeks in 1966 (Table I). The low recapture of Pelican Creek trout was probably due to the damaged Pelican Creek trap. The r values of the home group tended to be higher than those of the non-return group for blind, anosmic, and combined groups, but not for controls (Table XX). The mean directions of home and non-return groups were not significantly different.

TABLE XVII. Mean directions and vector lengths of float-tracked trout based on true North (uncorrected) and current direction as the zero direction (corrected).

Year	Category	No. tracked	Uncorrected		Corrected	
			Mean direction (*a*)	Vector length (*r*)	Mean direction (*a*)	Vector length (*r*)
			Clear Creek			
1965	Blind	18	88°	0.7044	3°	0.5231
	Control	21	79	0.2192	34	0.3326
	Combined	39	85	0.4422	16	0.4054
	Current drogue	6	59	0.7547		
1966	Blind	19	81	0.1919	26	0.0317
	Anosmic	19	49	0.4070	65	0.4021
	Control	18	97	0.2853	194	0.2163
	Combined	56	67	0.2671	90	0.1115
	Current drogue	11	289	0.4089		
			Cub Creek			
1965	Blind	6	325	0.8234	327	0.8342
	Control	5	354	0.9615	357	0.9180
	Combined	11	339	0.8585	344	0.8286
	Current drogue	2	355	0.9483		
			Pelican Creek			
1966	Blind	8	92	0.5722	20	0.5382
	Anosmic	8	59	0.5197	330	0.5358
	Control	8	64	0.7174	336	0.5303
	Combined	24	71	0.5847	349	0.4987
	Current drogue	4	74	0.7607		

A control (anesthetized only) trout from Clear Creek (Fig. 4, No. 1 — ripe female) was tracked from point B for 6 hr, 20 min on July 31, 1965; during this time she traveled 6.2 km (average speed 1.0 km/hr) ending about 60% of the distance from point B to Clear Creek. A blind trout (No. 2 — ripe female) was tracked 3 hr, 26 min on August 1, 1965 during which time she traveled 2.1 km (0.6 km/hr) in a southwesterly direction. The weather was clear and sunny during both these tracks. A non-anesthetized trout (No. 3 — ripe male) was tracked 3 hr, 56 min on May 31, 1966 during which time he traveled 3.1 km (0.8 km/hr), first northward, then eastward to the vicinity of a small island, and then westward. The weather was initially clear, changing to cloudy with light rain while the trout was near the island, and then clearing for the remainder of the time. This trout was tagged at the end of the tracking period and was recaptured in the homestream 11 days later.

ANGLER RETURNS

Twenty tags from Clear Creek trout and 13 from Cub Creek trout were returned by anglers (Table XXI). These trout had been released at points

TABLE XVIII. Mean directions and vector lengths of float-tracked trout based on true North (uncorrected) and sun azimuth as the zero direction (corrected).

Year	Category	No. tracked	Uncorrected		Corrected	
			Mean direction (a)	Vector length (r)	Mean direction (a)	Vector length (r)
			Clear Creek			
1965	Blind	26	85°	0.7319	327°	0.6212
	Anosmic	4	152	0.4261	48	0.4266
	Control	37	66	0.4322	294	0.4474
	Combined	67	79	0.5224	313	0.4665
	Sun azimuth	67	115	0.8896		
1966	Blind	19	81	0.1919	341	0.2370
	Anosmic	18	97	0.2853	351	0.3208
	Control	19	49	0.4070	294	0.3253
	Combined	56	67	0.2671	327	0.2654
	Sun azimuth	56	105	0.9443		
			Cub Creek			
1965	Blind	6	325	0.8234	181	0.7929
	Control	5	354	0.9615	222	0.8423
	Non-anesthetized	10	17	0.3562	306	0.3726
	Combined	21	0	0.4696	226	0.3926
	Sun azimuth	21	130	0.9266		
			Pelican Creek			
1966	Blind	8	92	0.5722	1	0.5523
	Anosmic	8	64	0.7174	328	0.5286
	Control	8	59	0.5197	334	0.7056
	Combined	24	71	0.5847	340	0.5785
	Sun azimuth	24	92	0.9978		

A, B, C, D, and E (Fig. 1). In general the distribution of angler recaptures reflected fishing pressure, which was concentrated along the western, northern, and northeastern shores. Two trout homed before angling recapture. Times from release to recapture ranged from 0.5 to 45 days within one season, and two opercle-tagged trout were recaptured just over 1 year after release. In general, opercle-tagged trout were at large longer (2.5–46 days) than those tagged with alligator clips (0.5–16.5 days). Recaptures were distributed widely in the heavily fished areas of the lake and were not clustered near the release points or the homestreams. No trout were recaptured in the southern portion of the lake, but fishing pressure there was extremely light.

DISCUSSION

Homing percentages and total recapture percentages of both Clear and Cub Creek trout were strikingly lower, and homing time was much less, in 1964 than in 1965 and 1966 (Table I). Either the handling procedure or the

TABLE XIX. Recaptures of Clear, Cub, and Pelican Creek trout tagged and released after float-tracking at point B, 1966. (Percentages in parentheses.)

Origin stream	Category	No. released	No. of recaptures			
			Homing	Straying	Angling	Total
Clear	Blind	18	8(44.4)	1(5.6)	0(0.0)	9(50.0)
	Anosmic	18	2(11.1)	0(0.0)	1(5.6)	3(16.7)
	Control	18	10(55.6)	0(0.0)	0(0.0)	10(55.6)
	Total	54	20(37.0)	1(1.9)	1(1.9)	22(40.8)
Cub	Blind	2	2(100.0)	0(0.0)	0(0.0)	2(100.0)
	Anosmic	2	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Control	1	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Total	5	2(40.0)	0(0.0)	0(0.0)	2(40.0)
Pelican	Blind	7	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Anosmic	7	1(14.3)	0(0.0)	0(0.0)	1(14.3)
	Control	8	0(0.0)	0(0.0)	0(0.0)	0(0.0)
	Total	22	1(4.5)	0(0.0)	0(0.0)	1(4.5)

TABLE XX. Comparison of mean directions and vector lengths of Clear Creek trout recaptured in the homestream with those not recaptured after float-tracking at point B, 1966.

Category	No. tracked	Mean direction(a)	Vector length(r)	Rayleigh test (z)[a]	Homestream test (R)[a]	Directions test (F)
Blind home	8	113°	0.4502	1.62	3.60	1.46
Non-return	9	22	0.1592	0.23	1.43	
Anosmic home	2	13	0.9903	–[b]	–[b]	<1
Non-return	14	25	0.3714	1.93	5.20	
Control home	10	62	0.4456	1.99	4.46	3.53
Non-return	7	146	0.5333	1.99	3.73	
Combined home	20	19	0.4068	3.31*	8.14*	<1
Non-return	30	31	0.1892	1.07	5.68	

[a]*Significant at $P = 0.05$.
[b]Sample too small for test.

lateness in the spawning season when the experiments were conducted in 1964, or both, were believed responsible. For opercle tagging in 1964 the trout had to be anesthetized and total time from netting to release was as much as 2 hr — three times as long as for alligator clip tagging in 1965 and 1966. Comparison of control (anesthetized only) and non-anesthetized trout in 1966 showed that anesthetic as such did not affect homing percentages or

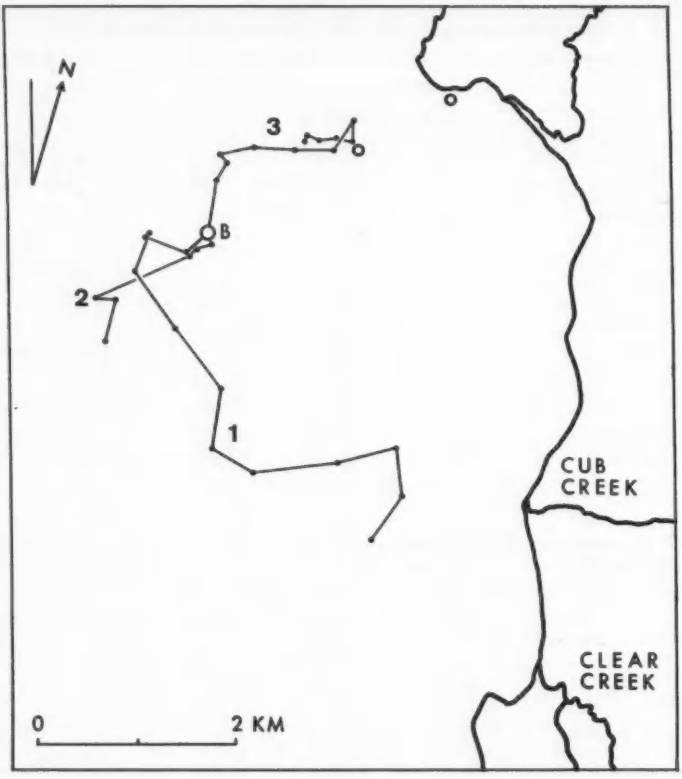

FIG. 4. Float-tracks of three Clear Creek trout beginning at point B. 1, control (anesthetized only) trout, July 31, 1965, 6 hr, 20 min; 2, blind trout, August 1, 1965, 3 hr, 26 min; 3, non-anesthetized trout, May 31, 1966, 3 hr, 56 min.

times. Black and Connor (1964) found that anesthetization of rainbow trout (with M.S. 222) did not change blood lactate or muscle glycogen, but Black and Barrett (1957) reported that even minimal handling and transportation for a 2-hr period caused increases in muscular activity and blood lactate in cutthroat and steelhead trout. Parker et al. (1963) emphasized any time taken to obtain a measurement may contribute greatly to fatigue.

The opercle tag may have contributed to mortality or aberrant behavior. Mechanical abrasion of the underlying gill tissue was apparent in most recaptured cutthroat trout with opercle tags. Rectangular sections of the posterior edge of the operculum were missing from many recaptured trout, indicating that tag loss may have been high. Marlborough (1963) reported opercle tag abrasion and loss in *Cyprinus carpio* and *Carassius carassius*. Miller (1957) stated that cutthroat trout behavior was affected by Petersen tags,

TABLE XXI. Distribution of tagged cutthroat trout recaptured by anglers during 1964, 1965, and 1966.

Recapture area in lake	No. of returns	Distances traveled (*km*)
Western portion	9	7.4–23.5
Northwestern portion	6	4.6–10.4
Outlet, Yellowstone River	3	7.8–10.4
Northeastern portion	9	2.0–5.2
Near Cub Creek	3	1.3–3.9
Near Clear Creek	3	0.2–7.7

and Clancy (1963) showed that swimming endurance of steelhead fingerlings tagged with Petersen tags was permanently reduced about half. On the other hand Gunning (1965) reported that movements of longear sunfish (*Lepomis megalotis*) in streams were not affected by opercle tags.

Greater loss of opercle tags than alligator clips would give an apparent lower return and faster homing time, since the slower trout would have more time to lose tags. No comparative tag loss information is available however.

In 1964, abnormally high run-off prevented adequate displacement experiments until after the peak of the spawning run. The delay caused by displacement may have allowed environmental conditions to develop which were not conducive to cutthroat trout migration and spawning. This would also result in an apparent faster return time of those recaptured. In 1966 a control (anesthetized only) group and a non-anesthetized group released about a week later than two similar groups had an average homing time only half as long. Thus homing times showed a real or apparent decrease as the migration season progressed.

The average homing times reported here are much slower than the fastest times. The fastest homing speeds, 19 cm/sec (0.7 km/hr), were recorded for Clear Creek trout released at point B. In terms of trout length these speeds ranged from 0.50 to 0.65 lengths (L)/sec. They are similar to those exhibited by three trout float-tracked for several hours (0.4–0.7 L/sec) by us, and to the average speeds of Clear and Cub Creek trout (0.59 L/sec and 0.48 L/sec respectively) float-tracked for 1 hr from a mid-lake point by Jahn (1966). These speeds are somewhat lower than the 0.9–1.7 L/sec for sockeye and coho salmon in actual up-river migration (Ellis, 1966). All of the above values are well below sustained swimming speeds obtained in the laboratory for sockeye salmon (3.0 L/sec) by Brett (1965) and trout (*Salmo irideus*) (2.0 L/sec) by Bainbridge (1962). However, in the case of cutthroat trout, a straight line journey is assumed for homing individuals so the distance estimate is minimal. Trout may have entered the trap some time before being recorded so the time estimate is maximal. The tracked trout were towing the Styrofoam floats, which probably reduced swimming speed.

Trout homed from just outside the stream mouth at about the same or even slower speed than those from much greater distances. The displacement

of migrating trout may cause physiological and behavioral changes resulting in delay while the trout begins a new sequence of events leading to migration and spawning. This delay may occur near the mouth of the stream, where salmonids are known to congregate before upstream migration. The three long-time float-tracks showed that trout can make fairly rapid and direct progress even while towing a float. The actual path and timing of homing travel need further investigation.

The amount of straying exchange for trout between Cub and Clear creeks during the in-season displacement experiments is higher than that reported by Cope (1957) for repeat homing experiments. Of his recaptures, 3.3% strayed as contrasted to 15.6% in the present study, and 0.0% during the natal homing studies of Ball (1955). During the experiments of Cope (1957) and Ball (1955), five and six streams, respectively, had fish traps, whereas in the present study only Clear and Cub creeks had effective traps. Natal and repeat homing favor the genetic separation necessary to produce and maintain the subpopulations of cutthroat trout in the Yellowstone Lake drainage reported by Cope (1957) and Bulkley (1963). Straying of first-time and repeat spawners prevents complete isolation of the various spawning runs. The distribution of angler recaptures (Table XXI) supports the generally accepted conclusion that the subpopulations of trout in Yellowstone Lake are not spatially segregated except during the spawning period, when the trout have ascended the tributaries. In-season homing and straying would not affect spawning season segregation of subpopulations, since in-season displacement is not a part of the cutthroat life history. Some portion of the straying may be an artifact due to "proving" suggested by Ricker (unpublished), in which a fish may ascend a "wrong" tributary some distance and then reject it. However, if a trap is across the stream, the fish is caught and recorded as a stray. This may well occur in Clear and Cub creeks, since the traps are close to the stream mouths.

The east-northeastward orientation of Clear Creek trout and the northward orientation of Cub Creek trout at point B in the present study were similar to the northeastward and northward orientations of Clear and Cub Creek trout, respectively, tracked from a mid-lake point by Jahn (1966). This was true even though the directions to Clear and Cub creeks from point B are 143° and 130°, respectively, and from the mid-lake point 93° and 73°, respectively. The orientation of Pelican Creek trout was also east-northeastward, but Pelican Creek is 325° from point B. Clear and Cub Creek trout tracked as long as 2 hr by Jahn (1966) from a point near the Clear and Cub Creek shore went generally eastward (shoreward).

Apparently the cutthroat trout exhibited a compass orientation (Type II) rather than a navigation or goal finding ability (Type III), since the direction of orientation was the same at different release points and was not in the direction of the homestream. Moreover, Clear and Pelican Creek trout oriented in the same direction even though their home-streams were in opposite directions. Perhaps an eastward or northward orientation is a feature of all spawning populations of cutthroat trout in Yellowstone Lake; however, no

trout from streams on the west side of the lake have been tracked. The ability to maintain a constant compass direction until shore or bottom is available for cues and then paralleling the shoreline would be a considerable improvement over random search in homing from open-water points in Yellowstone Lake.

The possibility exists that non-spawning trout may also have an orientation. White bass displaced from spawning areas and tracked from a mid-lake point in Lake Mendota, Wisconsin, showed a marked orientation toward their homespawning ground (Hasler et al., 1965; Gardella, MS, 1967), but non-spawners tracked from the same point also showed a strong orientation in the same direction (Gardella, MS, 1967).

Blind, anosmic, control (anesthetized only), and non-anesthetized cutthroat trout showed similar orientation. Blind and anosmic trout were able to home in the same percentage as the control and non-anesthetized trout, but the blind trout were much slower. Jahn (1966) for cutthroat trout, Hasler et al. (1958) for white bass, and Winn et al. (1964) for parrot fishes have all presented evidence for partial or complete loss of orientation under overcast skies. However, blind cutthroat trout were not disoriented.

Results obtained in this study with blind cutthroat trout and that of Jahn (1966) under overcast skies suggest that celestial cues may be used by cutthroat trout for orientation if available, but other orientation mechanisms may be used if vision of celestial cues is prevented. Groot (1965) showed that seaward migrating sockeye salmon smolts possess more than one orientation mechanism. Under clear skies, a celestial orientation (sun and polarized light) was used, and as clouds built up the dispersion of the orientation increased. Under complete overcast, however, orientation was again exhibited, and was attributed by Groot to non-celestial phenomena (X-orientation). In addition landmark orientation occurred. Winn et al. (1964) believed the sun and not the polarization pattern to be responsible for the orientation of parrot fishes. Cutthroat trout may orient at night, since Pacific salmon (Brett and Groot, 1963) are known to do so. Tracking of cutthroat trout at night and of trout whose internal clocks had been shifted would provide important information on celestial orientation.

Olfactory occlusion apparently did not prevent cutthroat trout from choosing the proper stream in Yellowstone Lake but it did prevent migrating silver salmon from making the proper choice at a stream fork (Wisby and Hasler, 1954). The displacement of anosmic trout should be repeated with an improved occlusion technique to provide conclusive results. Anosmic trout that were float-tracked, oriented as well as controls, in keeping with the hypothesis that odor could not play a directing role in orientation in large bodies of water (Hasler, 1966; Brett and Groot, 1963).

ACKNOWLEDGMENTS

Thanks are due Dr C. J. D. Brown, who directed the study and assisted in preparation of the manuscript, and to Dr R. M. Horrall and Messrs L. A.

Jahn and Q. J. Stober, who gave many suggestions and help in the field. Excellent cooperation was received from the National Park Service and Mr F. P. Sharpe and his crew of the U.S. Fish and Wildlife Service. Dr W. H. Sippel generously loaned a boat and house trailer for use in this study. Funds and equipment for the first year of the study were provided by the Cooperative Fisheries Unit; and the Department of Zoology and Entomology at Montana State University; by the Federal Water Pollution Control Administration (training grant # 1T1-WP-1) administered through Dr J. C. Wright; and by the Yellowstone Library and Museum Association through Mr J. M. Good. Funds for the second and third years of the study were supplied by grants from the National Science Foundation (grant # GB-3512) and the Office of Naval Research (grant # NR 301-854, contract nonr 4840) awarded to Dr C. J. D. Brown.

REFERENCES

BAINBRIDGE, R. 1962. Training, speed and stamina in trout. J. Exptl. Biol., **39**: 537–555.

BALL, O. P. 1955. Some aspects of homing in cutthroat trout. Proc. Utah Acad. Sci., **32**: 75–80.

BALL, O. P., AND O. B. COPE. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish Wildlife Serv., Res. Rept., **55**: 1–62.

BARDACH, J. E., AND J. CASE. 1965. Sensory capabilities of the modified fins of squirrel hake (*Urophycis chuss*) and searobins (*Prionotus carolinus* and *P. evolans*). Copeia, 1965(2): 194–206.

BARTLETT, M. S. 1937a. Properties of sufficiency and statistical tests. Proc. Roy. Soc. London Ser. A, **160**: 268–282.

1937b. Some examples of statistical methods of research in agriculture and applied biology. J. Roy Statis. Soc. Suppl., **4**: 137–183.

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Am. Inst. Biol. Sci., Wash. 57 p.

BENSON, N. G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish Wildlife Serv., Res. Rept., **56**: 1–33.

BLACK, E. C., AND I. BARRETT. 1957. Increase in levels of lactic acid in the blood of cutthroat and steelhead trout following handling and live transportation. Canadian Fish Culturist, **20**: 13–24.

BLACK, EDGAR C., AND ANNE R. CONNER. 1964. Effects of MS 222 on glycogen and lactate levels in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada, **21**(6): 1539–1542.

BRETT, J. R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). Ibid., **22**(6): 1491–1501.

BRETT, J. R., AND C. GROOT. 1963. Some aspects of olfactory and visual responses in Pacific salmon. Ibid., **20**(2): 287–303.

BULKLEY, R. V. 1961. Fluctuations in age composition and growth rate of cutthroat trout in Yellowstone Lake. U.S. Fish Wildlife Serv., Res. Rept., **54**: 1–31.

1963. Natural variation in spotting, hyoid teeth counts, and coloration of Yellowstone cutthroat trout, *Salmo clarki lewisi* Girard. U.S. Fish Wildlife Serv., Spec. Sci. Rept. — Fish., **460**: 1–11.

CLANCY, D. W. 1963. Effect of tagging with Petersen disc tags on the swimming ability of fingerling steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada, **20**(4): 969–981.

COPE, O. B. 1957. Races of cutthroat trout in Yellowstone Lake. U.S. Fish Wildlife Serv., Spec. Sci. Rept., **208**: 74–84.

DUNCAN, D. B. 1955. Multiple range and multiple F tests. Biometrics, **11**: 1–42.

ELLIS, D. V. 1966. Swimming speeds of sockeye and coho salmon on spawning migration. J. Fish. Res. Bd. Canada, **23**(2): 181–187.

FAGERLUND, U. H. M., J. R. MCBRIDE, M. SMITH, AND N. TOMLINSON. 1963. Olfactory perception in migrating salmon. III. Stimulants for adult sockeye salmon (*Oncorhynchus nerka*) in home stream waters. Ibid., **20**(6): 1457–1463.

FROST, W. E. 1963. The homing of charr *Salvelinus willughbii* (Günther) in Windermere. Animal Behaviour, **11**(1): 74–82.

GARDELLA, E. S. MS, 1967. The study of open-water orientation of white bass, *Roccus chrysops* (Rafinesque), by the use of ultrasonic tracking methods. M.Sc. Thesis. Univ. Wisconsin. 62 p.

GERKING, S. D. 1959. The restricted movement of fish populations. Biol. Rev., **34**: 221–242.

GREENWOOD, J. A., AND D. DURAND. 1955. The distribution of length and components of the sum of n random unit vectors. Ann. Math. Statis., **26**: 233–246.

GRIFFIN, D. R. 1952. Bird navigation. Biol. Rev., **27**: 359–393.

GROOT, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour, Suppl., **14**: 1–198.

GUNNING, G. E. 1965. A behavioral analysis of the movement of tagged longear sunfish. Progressive Fish-Culturist, **27**(4): 211–215.

HARA, T. J., K. UEDA, AND A. Gorbman. 1965. Electroencephalographic studies of homing salmon. Science, **149**(3686): 884–885.

HARTMAN, W. L., AND R. F. RALEIGH. 1964. Tributary homing of sockeye salmon at Brooks and Karluk lakes, Alaska. J. Fish. Res. Bd. Canada, **21**(3): 485–504.

HASLER, A. D. 1956a. Influence of environmental reference points on learned orientation in fish (*Phoxinus*). Z. Vergl. Physiol., **38**: 303–310.

1956b. Perception of pathways by fishes in migration. Quart. Rev. Biol., **31**(3): 200–209.

1960a. Homing orientation in migrating fishes. Ergeb. Biol., **23**: 94–115.

1960b. Guideposts of migrating fishes. Science, **132**(3430): 785–792.

1966. Underwater guideposts. Univ. Wisconsin Press, Madison, Wis. 155 p.

HASLER, A. D., H. F. HENDERSON, R. M. HORRALL, AND E. S. GARDELLA. 1965. Orientation of homing white bass (abstr.). Am. Zool., **5**(4): 383.

HASLER, A. D., R. M. HORRALL, W. J. WISBY, AND W. BRAEMER. 1958. Sun-orientation and homing in fishes. Limnol. Oceanog., **3**(4): 353–361.

HASLER, A. D., AND W. J. WISBY. 1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. Am. Naturalist, **85**(823): 223–238.

1958. The return of displaced large-mouth bass and green sunfish to a "home" area. Ecology, **39**(2): 289–293.

HELLE, J. H. 1966. Behavior of displaced adult pink salmon. Trans. Am. Fish. Soc., **95**(2): 188–195.

HORRALL, R. M. MS, 1961. A comparative study of two spawning populations of the white bass, *Roccus chrysops* (Rafinesque), in Lake Mendota, Wisconsin, with special reference to homing behavior. Ph.D. Thesis. Univ. Wisconsin. 181 p.

IDLER, D. R., J. R. MCBRIDE, R. E. E. JONAS, AND N. TOMLINSON. 1961. Olfactory perception in migrating salmon. II. Studies on a laboratory bio-assay for homestream water and mammalian repellent. Canadian J. Biochem. Physiol., **39**: 1575–1584.

JAHN, L. A. 1966. Open-water movements of the cutthroat trout (*Salmo clarki*) in Yellowstone Lake after displacement from spawning streams. J. Fish. Res. Bd. Canada, **23**(10): 1475–1485.

JOHNSON, W. E., AND C. GROOT. 1963. Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large, complex lake system. Ibid., **20**(4): 919–938.

LINDSEY, C. C., T. G. NORTHCOTE, AND G. F. HARTMAN. 1959. Homing of rainbow trout to inlet and outlet spawning streams at Loon Lake, British Columbia. Ibid., **16**(5): 695–719.

MARLBOROUGH, D. 1963. The unsuitability of monel metal opercular strap tags for tagging carp. Progressive Fish-Culturist, **25**(3): 155–158.

MCBRIDE, J. R., U. H. M. FAGERLUND, M. SMITH, AND N. TOMLINSON. 1964. Olfactory perception in juvenile salmon. II. Conditioned response of juvenile sockeye salmon (*Oncorhynchus nerka*) to lake waters. Canadian J. Zool., **42**: 245–248.

MCCLEAVE, J. D., L. A. JAHN, AND C. J. D. BROWN. 1967. Miniature alligator clips as fish tags. Progressive Fish-Culturist, **29**(1): 60–61.

MILLER, R. B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. J. Fish. Res. Bd. Canada, **14**(5): 687–691.

PARKER, R. R., E. C. BLACK, AND P. A. LARKIN. 1963. Some aspects of fish-marking mortality. Rappt. Procés-Verbaux Réunions Conseil Intern. Exploration Mer, **370**: 117–122.

PATTEN, B. C. 1964. The rational decision process in salmon migration. J. Conseil Conseil Perm. Intern. Exploration Mer, **28**(3): 410–417.

PLATTS, W. S. 1959. Homing, movements, and mortality of wild cutthroat trout (*Salmo clarki* Richardson) spawned artificially. Progressive Fish-Culturist, **21**(1): 36–38.

SAILA, S. B., AND R. A. SHAPPY. 1963. Random movement and orientation in salmon migration. J. Conseil Conseil Perm. Intern. Exploration Mer, **28**(1): 153–166.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill, New York. 481 p.

STEPHENS, M. A. 1962. Exact and approximate tests for directions. I. Biometrika, **49**: 463–477.

STUART, T. A. 1957. The migrations and homing behavior of brown trout (*Salmo trutta* L.). Scottish Home Dept., Freshwater Salmon Fish. Res., **18**: 1–27.

VLADYKOV, V. D. 1942. Precision with which speckled trout (*Salvelinus fontinalis*) return to the same spawning grounds. Canadian Field Naturalist, **56**(8/9): 134–136.

WATSON, G. S., AND E. J. WILLIAMS. 1956. On the construction of significance tests on the circle and the sphere. Biometrika, **43**: 344–352.

WINN, H. E., M. SALMON, AND N. ROBERTS. 1964. Sun compass orientation by parrot fishes. Z. Tierpsychol., **21**(7): 798–812.

WISBY, W. J., AND A. D. HASLER. 1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). J. Fish. Res. Bd. Canada, **11**(4): 472–478.

Primary Productivity in the Babine Lake System, British Columbia[1]

By David W. Narver

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Primary productivity in Babine Lake, British Columbia, as measured by the C^{14} in situ method in 1966 was slightly lower in the North Arm (outlet) and Morrison Arm (an inlet) than in the main lake region. An unusually high rate of photosynthesis at one part of the main lake in September may have been related to the decomposition of salmon carcasses in a nearby stream. Morrison Lake, a major tributary, was much lower in rate of photosynthesis, *p*H, alkalinity, compensation depth, and total dissolved solids than any part of Babine Lake. The rate of carbon fixation of Babine Lake was much less on a per unit area basis than those reported by other workers for the majority of 24 sockeye salmon lakes in southwestern Alaska but was similar to most per unit volume of the euphotic layer. Much of this difference is attributable to a shallower euphotic zone in Babine Lake. Ranked with the 24 Alaskan lakes, Babine was first in alkalinity, third in TDS, and fifth in *p*H.

The productivity measurements suggest that the carrying capacity for sockeye salmon per unit of nursery area of the main lake region is at least as great as that of the North Arm.

INTRODUCTION

Babine Lake (Fig. 1), a large, complex lake in the Northern Interior Plateau region of British Columbia (Northcote and Larkin, 1956), produces over 90% of the sockeye salmon that enter the Skeena River. The average number of adult sockeye salmon entering the Babine system from 1957 to 1966 was 616,000,[2] and at least an equal number were taken in the Skeena River gill-net fishery. Studies since 1955 have revealed that biomass of zooplankton and density of juvenile sockeye salmon contrast markedly between regions in the lake (Johnson, 1958, 1961, 1964). A relatively high density per acre of young sockeye is found annually in the Nilkitkwa–North Arm region, and a low density in the main lake region (Fig. 1). Conversely, the biomass of zooplankton is lower in the Nilkitkwa–North Arm region than in the main lake. Johnson (1961, 1964) showed that the zooplankton biomass was inversely correlated, at least in part, with the density of young sockeye.

Unpublished data from Johnson suggest that carrying capacity for juvenile sockeye per unit of nursery area is similar throughout the lake.[3] Furthermore, these data suggest that the Nilkitkwa–North Arm region may

[1]Received for publication April 17, 1967.

[2]Exclusive of small 1-year-in-the-ocean males (jacks) that are presumed to contribute little to spawning.

[3]Carrying capacity is used here as the number of juvenile sockeye per unit nursery area that can be nurtured to a quantity and quality of smolts that maximizes the adult return.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

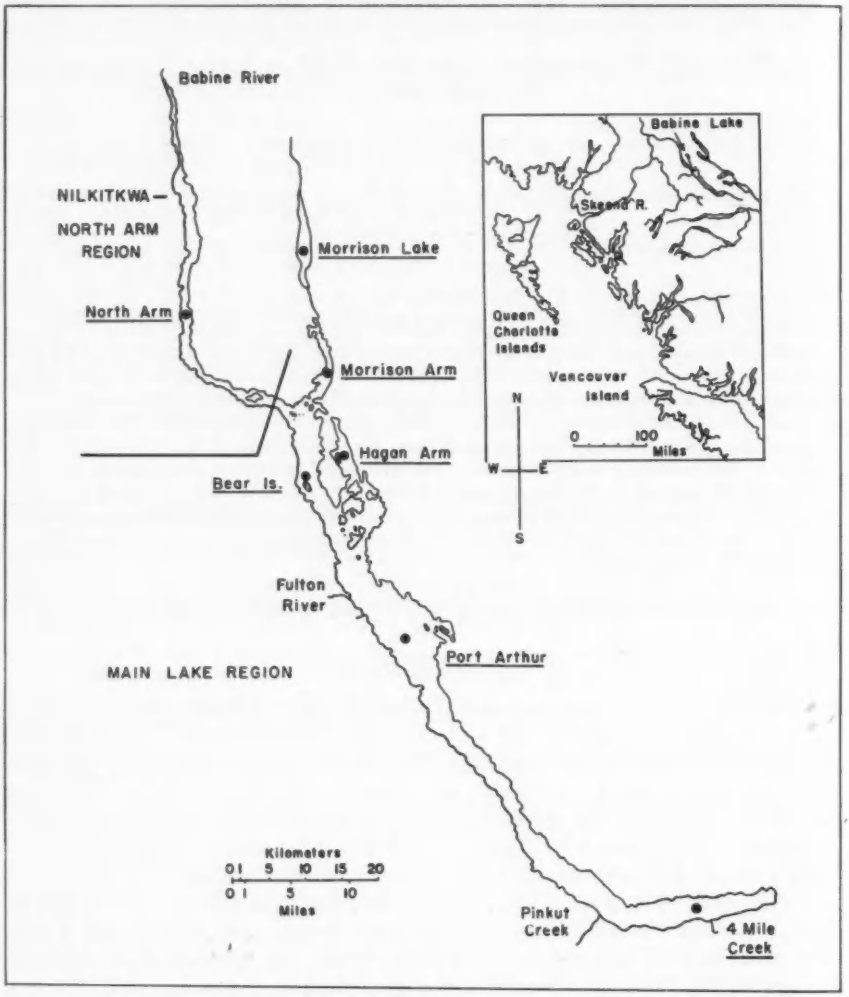

FIG. 1. Babine Lake, showing the locations of limnological stations and geographical features mentioned in the text.

occasionally approach this carrying capacity. For 1956–63 the mean density of August fingerlings (age 0+) in this region was 1110 per hectare (2750 per acre) (Department of Fisheries of Canada, MS, 1965), although Johnson (1965) suggested that maximum sockeye production in Babine Lake would be realized with an August fingerling population of 1477 per hectare (3650 per acre). In the main lake region the mean density was 222 per hectare (549

per acre) for the same period, so the main lake may be greatly underutilized for sockeye production.

In 1965 work was begun on a program to increase the density of sockeye fry in the main lake region (Department of Fisheries of Canada, MS, 1965). This program includes flow control and the construction of spawning channels on two major tributaries, the Fulton River and Pinkut Creek, and possible developments on Morrison River (Fig. 1). A major assumption was that the carrying capacity for young sockeye in the main lake region is similar to that of the Nilkitkwa–North Arm region.

The main purpose of this study in 1966 was to compare the rates of carbon fixation among areas of Babine Lake using the C^{14} in situ method; of primary interest was a comparison between the North Arm and the main lake region. Differences in production of phytoplankton would presumably affect production of juvenile sockeye salmon through the phytoplankton–zooplankton–sockeye food chain. For example, of 11 southwestern Alaska lake systems, the five with the highest rates of photosynthesis as indicated by C^{14} uptake produced adult sockeye salmon at highest levels per unit of lake area (Harry et al., 1967). Also Rupp and DeRoche (1965) concluded that biomass of fishes and growth of trout in three Maine lakes were related to primary productivity as measured by the C^{14} method.

The C^{14} technique of measuring the rate of photosynthesis of phytoplankton has been used widely in oceanographic studies and to a lesser extent in lakes since its introduction by Steemann Nielsen (1952). Since the technique measures the rate of carbon fixation within a bottle it only approximates the natural situation (Hooper et al., 1961). Also, interpretation of C^{14} results in terms of production by the phytoplankton is questionable. Rodhe et al. (1956) suggest that results are somewhat higher than net production. Recent studies suggest that C^{14} measures the amount of carbon retained in algae (Antia et al., 1963; Ryther and Menzel, 1965), and this may be less than true net production (McAllister et al., 1964). However, the technique does provide an approximate index of productivity that is useful in comparative work (Goldman, 1960; Hooper et al., 1961; Rupp and DeRoche, 1965; Harry et al., 1967).

METHODS

The field methods were basically those of Goldman (1960), who used the C^{14} technique in in situ experiments in Brooks Lake, Alaska. $Na^{14}CO_3$ was obtained from the Central Agency, Charlottenlund Castle, Denmark, in 1-ml ampoules with a mean specific activity of 3.53 μc (SD, 0.324; 7 ampoules analyzed by New England Nuclear Co., Boston, Mass.).

Water samples were collected at selected depths to 20 m using a 3-litre Van Dorn Sampler with a brass cylinder. Sample water was never held in the sampler longer than 1 min, so any toxic effect of brass on algae was minimized. In August and September experiments, about 123 ml of sample water was transferred to 125-ml Pyrex bottles with glass stoppers. Samples were kept

out of direct sunlight. After water samples were collected from all depths at a station, 1 ml of C^{14} carbonate was placed in each bottle with a 2-ml syringe with blunted needle. The ampoules were not rinsed, but no visible liquid remained. After inoculation the bottles were inverted several times and a rubber band was placed on each bottle to prevent the stopper from coming loose with pressure changes. Dark bottles were taped with black plastic tape and painted with black paint; before incubation a piece of black plastic sheet was secured over the stopper with a rubber band.

Bottle lines were fastened to the middle of a 15-ft aluminum bar with a float at either end. The stations were anchored at locations given in Fig. 1 for the duration of each experiment. Associated measurements were Secchi depth, solar radiation, weather observations, temperature profile, total dissolved solids, *p*H, and alkalinity. Standard incubation was for 4 hr starting about 1000 hr Pacific Daylight Time. Incubation depths and measurements obtained at each station were:

Depth (*m*)	1	2	3	4
Samples taken	Light, dark, alkalinity, *p*H, TDS	Light	Light, dark	Light

Depth (*m*)	5	7	10	15	20
Samples taken	Light, dark, alkalinity, *p*H	Light	Light, dark	Light, alkalinity, *p*H	Light, dark

Laboratory techniques were similar to those of Goldman (1960). After incubation, bottles were kept in the dark; filtration with HA Millipore filters (47 mm diam) was completed as soon as possible after the end of the experiment (not longer than 5 hr). Filtration vacuum was obtained by a hand pump and was probably nearly constant from sample to sample. After the sample was filtered, the funnel was washed with a few milliliters of 3% formalin. Filters were then dried in a desiccator and stored for later counting. A thin window counter by Baird Atomic was used (30% efficiency for 24-mm diam filters). An H2 Beckman *p*H meter was used for all *p*H determinations, including the 4.8 end point of the alkalinity titrations. Carbon fixation rates were calculated for the euphotic zone on both a unit volume and unit area basis. Calculation of both these rates and available C^{12} were made with a special computer program (FRN 291, Fisheries Research Institute, University of Washington). Compensation depth (lower limit of euphotic zone) was the depth at which C assimilated fell to 0.1 mg C/m^3.

Solar radiation measurements were made with a Belfort pyrheliograph, but only at Topley Landing (Fig. 1). Thus these records may not be realistic for experiments at distant stations such as North Arm or Four Mile Creek. Photosynthetic rate at the lake surface decreases at very high or low radiation intensity but there is a wide range of intensity within which little change in photosynthesis at the surface occurs (Edmondson, 1956). A day may have

to be very dark in order to reduce photosynthesis at the surface, but at depth photosynthesis may be markedly reduced. For example, on September 4 the midday solar radiation at Topley Landing was high because of cloudless sky (Table I) but clouds covered about $\frac{8}{10}$ of the sky at North and Morrison Arms. The low photosynthetic rates at these stations might have been partly due to reduced radiation at depth.

In limnological literature the rates of carbon fixation are frequently reported on a per day basis. To do this with the present data, 24-hr in situ experiments were conducted at the Port Arthur station in August and September on the same days as the midday 4-hr study. The rates of photosynthesis on both an area and volume basis are all about 2.2 times as great as for the simultaneous 4-hr experiments (Table I). With this factor August and September 4-hr rates can be adjusted to photosynthesis per 24 hr.

RESULTS AND DISCUSSION

Carbon Fixation in Different Parts of Babine Lake

The rates of carbon fixation on a per unit area basis were lower in North Arm and Morrison Arm than at any other station in Babine Lake in both August and September (Table I). Also, their fixation rates per unit volume of the euphotic zone were lower than for most other areas. Both areas tended to have slightly shallower Secchi depths than other parts of the lake (Table I). Compensation depths were the same throughout the lake in August, but North Arm was lower and Morrison Arm higher in September (Table I). The lower rate of carbon fixation in Morrison Arm is likely related to the apparent low level in Morrison Lake (see below). Morrison Arm, throughout the year, was lower in TDS (Table I).

The carbon fixation rates measured in both early and late June 1966 (Table I) are not comparable with other data because of differences in technique. The proportion of water filtered from each sample bottle was not recorded; in these experiments roughly 150 ml of each 200-ml sample was filtered. Thus the fixation rates are best used only for comparisons within either series of June experiments.

The late June series indicates higher rates of carbon fixation in the main lake than in North and Morrison Arm, just as in August and September. The early June series may have occurred before the spring phytoplankton bloom in the upper (south) end of the lake, accounting for the low rate of carbon fixation at Four Mile Creek. At the Four Mile Creek station on June 4 the transparency was highest and surface temperature the lowest of all measurements in 1966. The low *p*H at Port Arthur station on June 3 may be in error; this would cause the total available carbon and, in turn, carbon fixation rates, to be too high.

In early September the rates of carbon fixation at the Four Mile station were higher than in the rest of Babine Lake (Table I). Although rates were also high in late June and early August, the September activity might be

TABLE I. Summary of primary productivity measurements made in three months of 1966 in the Babine Lake system.

Station	Day	Time (*hr*)	Radiation (*ly/4 hr*)	Rate of C fixation (mg/m^2)	Rate of C fixation (mg/m^3)	pH	T. Alk. (*ppm* $CaCO_3$)	Avail. C^{12} (*per liter*)	Secchi (*m*)	Surface temp	Thermocline depth (*m*)	Comp. depth (*m*)	TDS (*ppm*)
August													
Four Mile	2	1000	180	30.976	3.439	7.4	34.77	9.39	4.5	15.0	–	9	72.0
Pt. Arthur	4	0950	205	35.408	3.899	7.5	35.95	9.35	4.0	15.6	–	9	71.5
(24-hr incubation)	(4)	(2200–3/8)	(457)	(78.641)	(8.738)								
North Arm	3	0915	161	17.439	1.933	7.5	33.48	8.70	3.5	15.6	–	9	72.5
Morrison Arm	3	1020	149	19.726	2.186	7.6	33.81	8.79	4.25	16.1	–	9	70.5
September													
Four Mile (A)	7	1022	124	41.765	4.426	7.5	34.57	8.99	5.25	13.5	17	9	–
Four Mile (B)	7	1025	124	34.818	3.783	7.7	34.20	8.55	5.25	13.5	17	9	68.5
Pt. Arthur	6	0950	106	18.036	1.948	7.4	33.37	9.01	5.0	12.0	0	9	68.0
(24-hr incubation)	(6)	(2200–5/9)	(251)	(40.238)	(4.471)								
North Arm	4	0910	175	14.559	2.018	7.2	33.47	9.37	3.5	13.5	12	7	–
Morrison Arm	4	1030	181	15.426	1.121	7.2	33.77	9.46	4.25	13.8	12	13	–
Hagan Arm	8	1020	180	18.778	2.013	7.5	34.09	8.86	4.5	13.9	10	9	69.0
Bear Island	8	0925	136	27.398	2.923	7.6	33.71	8.77	4.5	13.2	15	9	68.0
Morrison Lake	5	0930	(1/10 cloud)	10.071	1.620	7.2	25.10	7.03	3.5	12.8	–	6	57.0
June													
Four Mile	4	1015	(2/10 cloud)	7.827	.867	7.4	33.25	8.98	6.3	6.7	0	9	71.7
Pt. Arthur	3	1025	(2/10 cloud)	15.878	1.595	6.5	32.71	15.05	6.2	9.8	1	9	66.5
North Arm	6	1005	(6/10 cloud)	15.878	2.696	7.5	34.86	9.06	2.6	13.2	3	6	66.5
Morrison Arm	6	1140	(6/10 cloud)	8.204	1.306	7.4	32.87	8.87	3.0	16.1	4	6	64.2
Four Mile	22	1030	139	27.584	2.932	7.4	36.05	9.73	4.0	10.3	16	9	67.5
Pt. Arthur	23	0945	145	19.605	2.129	7.5	35.79	9.31	3.7	11.4	7	9	63.0
North Arm	21	1000	132	9.417	1.046	7.1	35.36	10.26	3.7	12.8	6	9	62.5
Morrison Arm	21	1125	140	8.091	1.279	7.2	31.84	8.92	3.3	14.7	6	6	57.5

explained by an increase in micronutrients resulting from the death and decomposition of the nearly 2000 sockeye salmon that spawned during August in Four Mile Creek, about 0.8 km from the station.

Morrison Lake

Observations were made on Morrison Lake on September 5, 1966, and consisted of one bottle line plus associated measurements. On an area basis the rate of carbon fixation was much lower than at any other station in September (Table I), primarily due to the shallow euphotic zone. Also the rate was lower on a volume basis than at any station in Babine Lake except Morrison Arm in the same period. Morrison Lake was also lower than Babine Lake in other indices of productivity, including *p*H, total alkalinity, total available carbon, compensation depth, and total dissolved solids (Table I).

Comparison with Alaskan Lakes

Primary productivity of Babine Lake in August and September 1966, can be compared with those of 24 major sockeye-producing lakes in southwestern Alaska, where a similar study was conducted in 1961 and 1962 for the same months (Harry et al., 1967). The rate of carbon fixation on a per unit area basis was much lower in Babine Lake than in all but three Alaska lakes; the rates in the 24 lakes ranged from 13 to 258 mg C/m^2 per 4 hr with a mean of 71.8 (Babine mean of 24.9). Fixation on a volume basis of the euphotic zone in Babine Lake (mean of 2.7) was slightly higher than for the majority of Alaskan lakes; the rates ranged from 1.0 to 33.4 mg C/m^3 per 4 hr but only six were over 2.5 and two over 5.9. Babine Lake, an inland lake, was higher in other indices of productivity than most of the Alaskan lakes, all maritime. Ranked with these lakes, Babine was first in alkalinity, third in TDS, and fifth in *p*H.

Variability

Two complete bottle lines were incubated about 150 m apart at Four Mile station on September 7. The results suggest a rather high between-sample variation since one sample was about 17% higher in fixation rate on an area basis than the other (Table I).

An indication of year-to-year variability that might be expected at Babine Lake can be obtained from studies at Aleknagik Lake, Alaska (Dr R.L. Burgner, personal communication). From 1963 to 1966 in the period June to September the means (mg C/m^2 per 4 hr) for one station were 63.3 (9 experiments), 70.3 (3), 47.8 (4), and 57.3 (6).

CONCLUSIONS

In late June, August, and September, North Arm and Morrison Arm had somewhat lower rates of carbon fixation than the other stations in Babine Lake. This supports the assumption, based on the density of juvenile sockeye

and on biomass of zooplankton, that the carrying capacity per unit of nursery area in the main lake is at least as great as that of the North Arm. Measures designed to produce more sockeye fry in the main lake region are already under way (Department of Fisheries of Canada, MS, 1965).

ACKNOWLEDGMENTS

Mr B. W. Chernoff assisted in the field work; Mr K. Stephens helped to implement the study; and Messrs C. D. McAllister, F. C. Withler, and Dr W. E. Ricker read the manuscript and provided valuable criticisms.

REFERENCES

ANTIA, N. J., C. D. MCALLISTER, T. R. PARSONS, K. STEPHENS, AND J. D. H. STRICKLAND. 1963. Further measurements of primary production using a large-volume plastic sphere. Limnol. Oceanog., **8**(2): 166–183.

DEPARTMENT OF FISHERIES OF CANADA. MS, 1965. Proposed sockeye salmon development program for Babine Lake. Pacific Area, Vancouver. 53 p.

EDMONDSON, T. E. 1956. The relation of photosynthesis by phytoplankton to light in lakes. Ecology, **37**(1): 161–174.

GOLDMAN, C. R. 1960. Primary productivity and limiting factors in three lakes of the Alaska Peninsula. Ecol. Monographs, **30**: 207–230.

HARRY, G. Y., W. F. ROYCE, C. J. DICOSTANZO, R. L. BURGNER, W. L. HARTMAN, O. A. MATHISEN, AND R. J. ELLIS. 1967. Summary report of studies on the optimum escapement of sockeye salmon in southwestern Alaska, 1961–62. U.S. Bur. Comm. Fish., Bull. (In press.)

HOOPER, F. F., M. A. PODOLIAK, AND S. E. SNIESZKO. 1961. Use of radioisotopes in hydrobiology and fish culture. Trans. Am. Fish. Soc., **90**(1): 49–57.

JOHNSON, W. E. 1958. Density and distribution of young sockeye salmon (*Oncorhynchus nerka*) throughout a multibasin lake system. J. Fish. Res. Bd. Canada, **15**(5): 961–982.

1961. Aspects of the ecology of a pelagic, zooplankton-eating fish. Verh. Intern. Verein. Limnol., **14**: 727–731.

1964. Quantitative aspects of the pelagic, entomostracan zooplankton of a multibasin lake system over a 6-year period. Ibid., **15**: 727–734.

1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Intern. Verein. Limnol., **13**: 66–87.

MCALLISTER, C. D., N. SHAH, AND J. D. H. STRICKLAND. 1964. Marine phytoplankton photosynthesis as a function of light intensity: a comparison of methods. J. Fish. Res. Bd. Canada, **21**(1): 159–181.

NORTHCOTE, T. G., AND P. A. LARKIN. 1956. Indices of productivity in British Columbia lakes. Ibid., **13**(4): 515–540.

RODHE, W., R. A. VOLLENWEIDER, AND A. NAUWERICK. 1956. The primary production and standing crop of phytoplankton. *In* A. A. Buzzati-Traverso [ed.] Perspectives in marine biology. Univ. Calif. Press, Berkeley and Los Angeles. p. 299–322.

RUPP, R. S., AND S. E. DEROCHE. 1965. Standing crops of fishes in three small lakes compared with C^{14} estimates of net primary productivity. Trans. Am. Fish. Soc., **94**(1): 9–25.

RYTHER, J. H., AND D. W. MENZEL. 1965. Comparison of the ^{14}C-technique with direct measurement of photosynthetic carbon fixation. Limnol. Oceanog., **10**(3): 490–492.

STEEMANN NIELSON, E. 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. J. Conseil Conseil Perm. Intern. Exploration Mer, **18**: 117–140.

Micro-Zooplankton in the Euphotic Zone at Five Locations Across the California Current[1]

By J. R. Beers and G. L. Stewart

Institute of Marine Resources, University of California, San Diego La Jolla, California

ABSTRACT

Quantitative samples of the plankton which passed 202-μ mesh filter cloth were collected with a pumping system at five locations from the slope waters of the Pacific Ocean off San Diego to across the California Current.

A general decrease in the numbers of micro-zooplankton, averaged over the depth of the euphotic zone, was found from the slope waters (310,000/m^3, Station I) to the site farthest offshore (99,000/m^3, Station V). At the various sites Protozoa accounted for between 59% and 83% of the total numbers, but only 18–23% of the total micro-zooplankton volume. The calculated volumes of the micro-zooplankton ranged from 22.9 mm^3/m^3 (Station I) down to 6.3 mm^3/m^3 (Station V).

INTRODUCTION

The development of meaningful models of oceanic food chains requires a knowledge of the abundance and biomass of all planktonic organisms. However, the mesh size in nets commonly used for quantitative zooplankton studies allows the small forms to pass through and these are overlooked by the marine ecologist. Though the smaller zooplankton have been studied much less than the larger forms, the findings suggest that the small organisms may have a significant role in certain marine communities. Lohmann (1908), working in the Kiel Fjord, showed that approximately 50% of the annual average biomass consisted of small metazoans, protozoans, eggs, and larvae retained on No. 20 (76-μ mesh) netting but not held by a No. 3 (333-μ mesh) net. Data presented by Hansen and Andersen (1962) on zooplankton abundance as calculated from Hensen net (No. 3 mesh silk) tows and 8-liter water bottle samples filtered through No. 25 (64-μ) silk showed a large fraction of the zooplankton was not captured by the net. For example, the average catches of organisms per unit volume of water for the Hensen net relative to the water bottle in 14 sets of samples from the Kattegat were: non-copepod Crustacea, 64%; copepods, 34%; animals other than Crustacea, 19%; and nauplii, <0.03%. Allen (1939) noted the relatively great abundance of small copepods in water samples for phytoplankton studies collected at various times over a year from a series of locations in the eastern Pacific extending 140 miles seaward at the latitude (approximately 35°N) of San Luis Obispo, California. Population densities ranged from 10,000 to 30,000 naupliar and post-naupliar forms per cubic meter.

[1]Received for publication March 7, 1967.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

In the present study the micro-zooplankton were sampled quantitatively at several oceanic locations across the California Current. A submersible pump system with a deck-mounted plankton collecting unit was assembled for this purpose (Beers et al., 1967). The system is capable of pumping water at a rate of approximately 150 liters/minute from any depth in the upper 100 m while being towed at approximately 3 knots. The integrated plankton samples thus obtained were representative of the water mass sampled.

In addition to analyses of the numbers of animals in the samples, volume estimates of the micro-zooplankton populations were made and compared with estimates for the larger zooplankton derived from data from the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program. Very heavy sea conditions encountered at all stations except one on our cruise made it necessary to omit the net tows which had been planned for direct comparisons with the pump samples.

"Micro-zooplankton" in this paper is defined as all animal forms which will pass a 202-μ mesh filter cloth. This is from the size classification of Dussart (1965), who proposed the use of "ultramicroplankton" for organisms from 2 to 20 μ and "microplankton" for the size range from 20 to 200 μ.

MATERIALS AND METHODS

Field Sampling

Microplankton samples were collected with the pumping system from five locations (Fig. 1) at 60–180 mile intervals from the slope waters of the Pacific Ocean off San Diego to across the California Current during a cruise of the *R. V. Horizon*, December 9–16, 1965. Although all sampling sites were in the oceanic province, Stations I and II were on the continental slope whereas the depth of the water column at the other locations exceeded 3500 m. At each station a series of replicate $1\frac{1}{2}$–$2\frac{1}{2}$-hr traverses of 10–14 km were made while pumping water from various depth intervals through the euphotic zone. During the sampling within each depth interval the pump was lowered and raised in four or five steps, each of approximately 15-min duration. This is illustrated in Fig. 2 for the sampling at Station III. The depths sampled were determined primarily by the temperature structure and the depth of the euphotic zone as determined from bathythermograph records and Secchi disc readings at each site. Some differences in the sampling program at the various stations (Table I) were necessitated because of the heavy seas encountered. The depths of the traverses were estimated on the basis of a relationship between the length of hose overboard, the speed of the boat, and the depth of the pump which was determined previously when the pumping system included an operational depth transducer. All sampling was done during daylight hours so as to avoid peak periods of zooplankton vertical migration. At Station IV a short circuit in the wiring to the pump motor forced the termination of pumping midway during the first traverse.

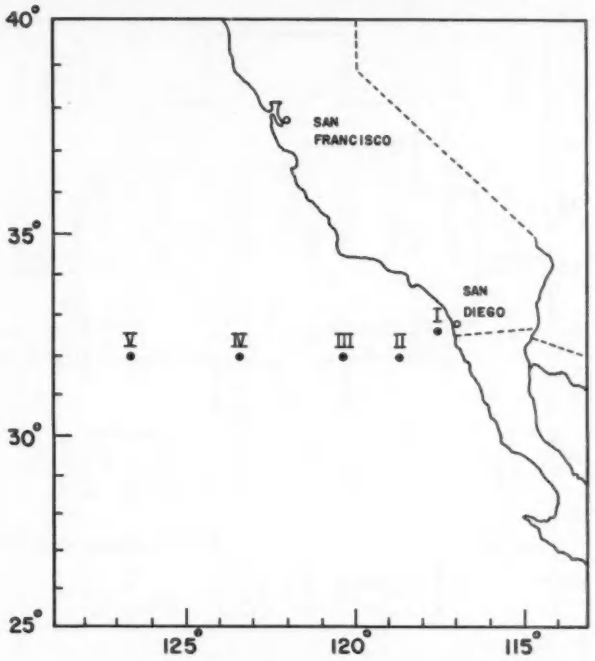

FIG. 1. The locations of the five stations where microplankton samples were collected (R.V. *Horizon*, December 10–16, 1965).

SIZE CLASSES

The set of filter cloths used in the deck-mounted collecting unit allowed for the separation of three size classes of microplankton: (1) organisms passing a 35-μ mesh cloth (−35); (2) organisms retained on the 35-μ cloth but passing 103-μ mesh (+35); and (3) those retained on the 103-μ cloth but passing a 202-μ cloth (+103). The 202-μ filter cloth provided a barrier to exclude larger organisms. The plankters in the −35 fraction were sampled by taking 500-ml aliquots of filtrate from the base of the collecting unit at approximately 5-min intervals throughout each traverse, mixing them thoroughly and saving a fraction, usually less than 1 liter. All samples were preserved in neutral-buffered formalin, the final concentration being approximately 5%.

COUNTING METHODS

Zooplankton in the −35 samples were counted in two or three 100-ml or 200-ml aliquots at a magnification of 100× using a phase-contrast microscope after concentration of the material on Millipore[2] filters by the "cleared" filter technique of Holmes (1962). Since ciliates other than tintinnids were

[2]Registered trademark, Millipore Filter Corporation, Bedford, Mass.

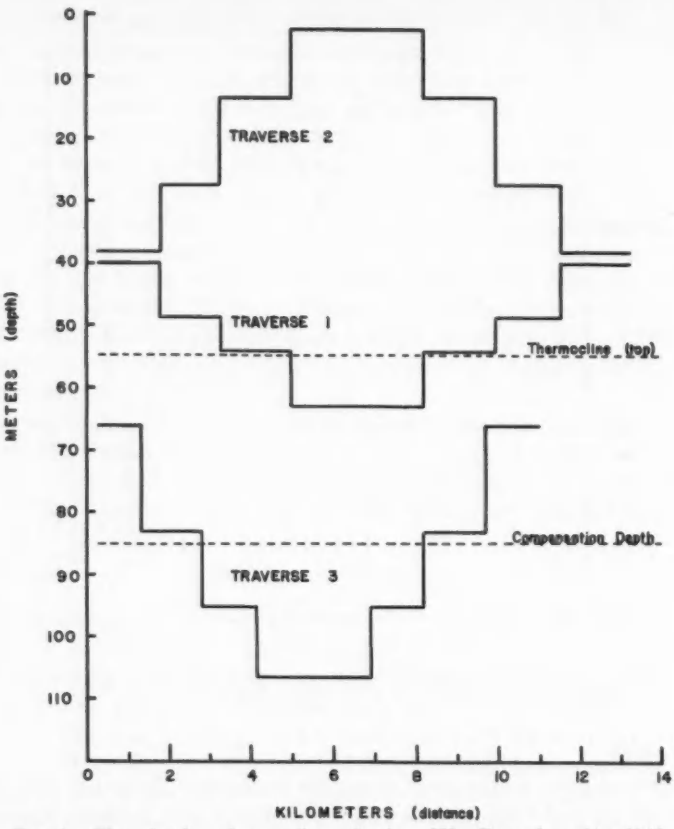

FIG. 2. The depths of sampling, Station III, December 11, 1965.

not easily recognizable on the "cleared" filter slides, they were counted in separate 100-ml aliquots of the samples by the inverted microscope method of Utermöhl (1931) at a magnification of 160×.

Numerical abundances of the zooplankton in the +35 and +103 samples were determined by the method of Utermöhl (1931). Magnifications used were 100× and 63×, respectively. Generally several aliquots (0.5–1.0 ml for the +35 and 5–10 ml for the +103 samples) of the concentrated material, removed from the thoroughly mixed sample with a wide-mouth, straight-bore pipette, were counted from each sample until 100 individuals of the major groups were enumerated.

The numbers of organisms counted in the +35 samples represented those from between 20 and 70 liters of the pumped water whereas the organisms counted in the +103 samples were the concentrated samples from approximately 0.25 to 1 m^3 of the pumped water.

TABLE I. Station locations and sampling program, R.V. *Horizon*, December 9–16, 1965.

Station	Date	Position	Total water depth (*m*)	Approx euphotic zone depth (*m*)	Traverse no.	Depths sampled (*m*)	Distance sampled (*km*)	Time (*hours*)	Volume water pumped (m^3)
I	Dec. 16	32°31′N 117°38′W	730	42	1	10–57	10.9	0833–1033	18.19
					2	66–112	13.5	1047–1247	18.19
II	Dec. 10	32°00′N 118°46′W	1010	65	1	10–20	10.5	0825–0952	12.55
					2	2	14.4	1028–1158	13.07
					3	36–65	10.2	1352–1528	13.15
III	Dec. 11	32°00′N 120°21′W	3750	84	1	40–62	13.1	0749–0949	17.57
					2	2–38	13.1	1003–1203	17.17
					3	66–107	10.9	1333–1533	17.99
IV	Dec. 12	32°00′N 123°29′W	4210	100	1	5–55	11.3	0943–1135	16.02
V	Dec. 13	32°00′N 126°38′W	3840	100	1	10–62	14.1	0830–1100	22.44
					2	72–130	12.6	1116–1346	22.94

The possible sub-sampling and counting errors were believed to be generally small. A comparison of sub-sampling with the straight-bore pipette and a Stempel pipette, both of 1-ml volume, showed no marked differences in the numbers and types of organisms that were taken. The chi-square test for randomness was applied to six major groups and seven species in a count of six replicate subsamples from the +35 samples and to four major groups and the dinoflagellate *Ceratium* sp. from the +103 samples of Station III, traverse #3. The results were not significant at $P = 0.05$ for any of the organisms except the diatom *Asterolampra* in the +35 samples. Thus, the hypothesis of random distribution, according to the Poisson law, was not disproved to any serious extent in the subsampling procedure for these size fractions.

All loricae and shells of tintinnids and radiolarians were counted since it is probable that many of these forms are readily separated from their "house" by stress conditions during the collecting and preserving of the samples. Only complete specimens of the other zooplankton groups were enumerated.

Data Presentation

The data are reported as the numbers of organisms per cubic meter and are rounded to two significant figures. Since the volume of water examined and the actual numbers of organisms counted were small in the −35 samples, confidence limits, based on the numbers of organisms counted, were calculated for each taxonomic group in the three size classes of samples. These were determined from the graphs of Holmes and Widrig (1956) for groups where the counts were less than 100 and calculated as ± twice the square root of the number observed where 100 or more individuals were counted.

To compare directly the different locations sampled, the results are presented in the form of integrated and averaged values over the estimated depth of the euphotic zone (3 × Secchi depth, Table I) at each station. For Station IV, the average values obtained for the single traverse, i.e. the upper 55 m, are included in the results although the depth of the euphotic zone was estimated to be approximately 100 m.

Complete data records for all traverses at each station, including data on the numerical abundance of the phytoplankton in the samples, are on file at the Institute of Marine Resources, University of California, San Diego.

RESULTS

A general decrease in the numbers of micro-zooplankton was found from the slope waters to the station farthest offshore (Table II). At all stations the number of organisms determined for the −35 samples was greater than those retained by the filter cloths. The ratio of the numbers in the samples passing the 35-μ mesh cloth to the total of the +35 and +103 samples varied from 5.6:1 (Station IV) to 9.8:1 (Station II) and averaged 7.4:1 (Table III).

TABLE II. Integrated and averaged numbers (and, in parentheses, confidence limits) of the various groups of micro-zooplankton per cubic meter over the depth of the euphotic zone in the three size classes of organisms.

Group	Station (no. per m²) I	II	III	IV	V
			—35 samples		
Protozoa					
Foraminifera	(29,000–80,000) 50,000	(16,000–52,000) 30,000	(30,000–72,000) 47,000	(15,000–53,000) 29,000	(4,000–31,000) 13,000
Radiolaria	(48,000–110,000) 72,000	(34,000–78,000) 51,000	(36,000–89,000) 59,000	(16,000–58,000) 32,000	(11,000–43,000) 23,000
Tintinnidae	(2,000–23,000) 8,000	(23,000–63,000) 39,000	(3,000–18,000) 7,000	(<1,000–15,000) 3,000	–
Ciliata other than Tintinnidae	(12,000–110,000) 42,000	(11,000–100,000) 39,000	(17,000–120,000) 53,000	(<1,000–59,000) 11,000	(4,000–82,000) 25,000
Metazoa					
Copepoda (post-naupliar)	(40,000–95,000) 64,000	(25,000–62,000) 38,000	(6,000–32,000) 15,000	(9,000–42,000) 21,000	(6,000–35,000) 14,000
Copedoda (naupliar)	(20,000–61,000) 37,000	(10,000–29,000) 18,000	(2,000–22,000) 7,000	(8,000–37,000) 19,000	(3,000–25,000) 10,000
Heteropoda and Pteropoda	–	(1,000–19,000) 6,000	(2,000–20,000) 6,000	(8,000–37,000) 19,000	(<1,000–5,000) 1,000
			+35 samples		
Protozoa					
Foraminifera	(1,600–3,000) 2,200	(500–1,500) 900	(1,300–2,100) 1,700	(1,200–2,100) 1,600	(880–1,500) 1,100
Radiolaria	(3,700–5,500) 4,600	(2,800–4,700) 3,600	(6,500–8,100) 7,300	(2,900–4,100) 3,500	(3,200–4,300) 3,700
Tintinnidae	(7,400–9,900) 8,700	(9,300–11,000) 10,000	(7,700–9,400) 8,500	(6,700–8,500) 7,700	(1,500–2,200) 1,900

(*Continued*)

TABLE II. Integrated and averaged numbers (and, in parentheses, confidence limits) of the various groups of micro-zooplankton per cubic meter over the depth of the euphotic zone in the three size classes of organisms. — (*Concluded*)

Group	Station (no. per m³)				
	I	II	III	IV	V
Metazoa					
Copepoda (post-naupliar)	(6,800–9,200)	(1,800–3,400)	(3,400–4,500)	(3,900–5,200)	(2,300–3,200)
	8,000	2,500	3,900	4,600	2,700
Copepoda (naupliar)	(5,000–7,100)	(2,100–3,800)	(2,400–3,500)	(3,300–4,600)	(2,100–2,900)
	6,000	2,900	3,000	4,000	2,500
Heteropoda and Pteropoda	(1–250)		(20–220)	(100–450)	(7–94)
	44	–	80	240	30
			+103 samples		
Protozoa					
Foraminifera	(45–120)	(3–26)	(17–46)	(17–46)	(38–71)
	76	10	30	29	52
Radiolaria	(210–340)	(51–110)	(200–270)	(120–180)	(170–230)
	270	73	240	150	190
Tintinnidae	(210–350)	(27–75)	(46–84)	(33–69)	(32–61)
	270	47	64	48	45
Metazoa					
Copepoda (post-naupliar)	(2800–3200)	(1100–1300)	(1200–1400)	(1700–1900)	(710–830)
	3,000	1,200	1,300	1,800	770
Copepoda (naupliar)	(360–520)	(70–137)	(96–150)	(170–240)	(100–150)
	440	99	120	200	130
Other Crustacea	(4–39)	(<1–8)	(1–11)		(<1–3)
	15	1	4	–	1
Chaetognatha	(2–33)		(<1–7)	(3–19)	(7–23)
	11		2	9	13
Heteropoda and Pteropoda	(26–83)	(20–60)	(38–74)	(11–33)	(16–40)
	49	36	53	20	26
Polychaeta (incl. larvae)	(1–27)	(<1–16)			
	8	4			

TABLE III. Numerical abundance and estimated volumes of Protozoa, Metazoa, and all micro-zooplankton in the three size classes of the plankton samples collected at the five locations.

	Protozoa				Metazoa				Total zooplankton			
Station	−35	+35	+103	Total	−35	+35	+103	Total	−35	+35	+103	Total
	No. per m³				*No. per m³*				*No. per m³*			
I	170,000	16,000	620	190,000	100,000	14,000	3,500	120,000	270,000	30,000	4,100	310,000
II	160,000	15,000	130	180,000	62,000	5,400	1,300	69,000	220,000	20,000	1,400	240,000
III	170,000	18,000	330	190,000	28,000	7,000	1,500	37,000	200,000	25,000	1,800	230,000
IV	75,000	13,000	230	88,000	59,000	8,800	2,000	70,000	130,000	22,000	2,200	150,000
V	61,000	6,700	290	68,000	25,000	5,200	940	31,000	86,000	12,000	1,200	99,000
	Volume (mm³/m³)				*Volume (mm³/m³)*				*Volume (mm³/m³)*			
I	3.3	0.6	0.1	4.0	10.0	2.8	6.1	18.9	13.3	3.4	6.2	22.9
II	2.7	0.6	<0.1	3.3	7.8	1.1	2.2	11.1	10.5	1.7	2.2	14.4
III	3.0	0.6	0.1	3.7	4.4	1.4	2.5	8.3	7.4	2.0	2.6	12.0
IV	1.7	0.5	0.1	2.3	10.1	1.8	3.4	15.3	11.8	2.3	3.5	17.6
V	0.9	0.2	0.1	1.2	2.5	1.0	1.6	5.1	3.4	1.2	1.7	6.3

PROTOZOA

The Protozoa were more abundant than metazoan forms at each location, varying between 59% (Station IV) and 83% (Station III) of the total animals. Of the three size classes of micro-zooplankton, Protozoa were the more abundant forms in the −35 and the +35 samples and Metazoa in the +103 fractions.

Three major protozoan groups were represented in the samples — the orders Radiolaria and Foraminifera of the class Sarcodina and the order Spirotricha of the class Ciliata.

More than 25 different radiolarians, mainly nassellarian and spumellarian types, were found. Identification of these, even to genus, was difficult since many were immature forms with only the cephalis and a relatively small part of the skeleton seen. Tentative identifications of the predominant forms encountered were: *Lithomelissa cf. thoracites* Haeckel, *Theoconus cf. zancleus* (Müller) (mainly immature forms with varying amounts of material added beyond the first body constriction), and *Peridium* sp.

The Foraminifera were represented by relatively few forms. Predominant among these were members of the Globigerinidae.

The spirotrichous ciliates included representatives of the Tintinnidae (suborder Oligotricha) and species of *Lohmanniella*, *Strombidium*, and *Laboea*. These latter were all small forms which passed the 35-μ cloth and were considered as "Ciliata other than Tintinnidae" in Table II. A total of 19 genera of tintinnids were recognized. Of these, seven were found in the −35 samples. *Dictyocysta* spp. were the most abundant in this size sample. The three species of *Dictyocysta* seen were of similar size and had loricae with an average length of approximately 55 μ and average bowl diameter of 40 μ. These were identified tentatively as *Dictyocysta dilatata* Brandt, *D. reticulata* Kofoid and Campbell, and *D. elegans* Ehrenberg. Other forms found in the −35 fractions included a species of *Codonella* having a bowl diameter of approximately 40 μ and *Salpingella* sp. with a length of about 300 μ and a diameter of 15–20 μ. Genera represented throughout the +35 and +103 samples and often in relatively large numbers included *Codonella*, *Epiplocylis*, *Eutintinnus*, *Proplectella*, *Salpingella*, *Xystonella*, and *Xystonellopsis*.

METAZOA

Metazoa in the −35 and +35 samples were crustaceans (postnaupliar and naupliar copepods) and molluscs (heteropods and pteropods). Other groups recorded from the +103 samples included "other Crustacea" (mainly ostracods), chaetognaths, and polychaetes including larval forms.

Copepods, including nauplii, were the most numerous Metazoa at all stations and in all size fractions sampled. They accounted for approximately 82% (Station III) to more than 99% (Station I) of the total number of Metazoa at the different locations. The only other group of any numerical importance was the heteropods and pteropods which comprised an estimated 17% by number of the total metazoan population at Station III.

Relatively abundant copepods included species of *Microcalanus*, *Clausocalanus*, *Paracalanus*, *Oithona*, and *Microsetella*. Naupliar forms were more numerous and composed a notably larger per cent of the total metazoans in the −35 and +35 samples than in the +103 samples. The station nearest to shore showed the largest numbers of copepods in all three size fractions. With the exception of low numbers in the +35 and +103 samples at Station II, there was a general decrease from east to west across the California Current.

Members of the heteropod genus *Atlanta* were abundant relative to other heteropod and pteropod forms.

DISCUSSION

Although knowledge of the numerical abundance of the various groups of micro-zooplankton is of importance in providing information on the animal population structure in marine communities, it can be misleading and of relatively little value as an index of the standing stock for trophodynamic considerations of marine food chain ecology. Paasche (1960), for example, has shown a bias favoring the smaller forms in using numerical abundance as an index of the standing stock of phytoplankton.

Volume Estimates

To provide estimates of the standing stocks of the micro-zooplankton which would not be prejudiced by the dissimilar sizes of the forms within any group, we made volume estimates based on two dimensional measurements of the various animals in the three size classes sampled and approximations of their shape to standard geometrical configurations. At least 20 individuals of each major group in the different size classes, picked at random from all traverses, were measured. Radiolarians and tintinnids were approximated to cones. In both groups it was assumed that the volume of the living animal is 50% of the shell or lorica volume. Copepods were considered to be double cylinders (cephalothorax and abdomen) with the abdomen length and width taken as one-third of the measurements for total length and width. Nauplii were regarded as simple cylinders. Heteropods, which generally lie on their sides in the settling chambers, were estimated to be cylinders with the height (altitude) taken to be equal to the radius. The "other Crustacea," mainly ostracods, were considered to be ellipsoidal in shape. Although chaetognaths could be enumerated by the presence of their jaws in the samples, they were omitted from the volume estimates since it was believed that they would have been retained on the 202-μ cloth if the bodies had been intact.

Omitting the results of the aborted Station IV, the data (Table III) show a decrease in volumes from the slope (Station I, 22.9 mm^3/m^3) to across the California Current (Station V, 6.3 mm^3/m^3). At all sites and for all size groups the volume of the metazoan population was markedly larger than that of the protozoans although the latter were numerically greater in each case. The total protozoan volume ranged from approximately 18% to 32% of the total animal volume at the various sites.

The calculated volumes of the micro-zooplankton were compared (Table IV) with estimates of the volumes of large zooplankton from CalCOFI program data (Thrailkill, 1956, 1957, 1959, 1961, 1963, and unpublished results). The estimates were determined by averaging all data available for the months

TABLE IV. A comparison of the estimated volumes of the micro-zooplankton with the estimated volumes of the larger zooplankton.

Station	Estimated volume of larger zooplankton from CalCOFI data (mm^3/m^3)	Estimated volume of micro-zooplankton (mm^3/m^3)	Percentage micro-zooplankton volume of larger zooplankton volume (%)
I	76	22.9	30
II	66	14.4	22
III	105	12.0	11
IV	131	17.6	13
V	61	6.3	10

of November, December, and January during the 10-year period from November 1956 through January 1966 at the CalCOFI grid stations within a 60-mile radius of each site we sampled. (For the year of this study only a limited amount of data is available for January 1966 and none is available for November or December 1965.) The quantity of data available for the calculation of the averages varied widely among the stations, with relatively large amounts available for stations I, II, and III but very few figures for stations IV and V. The CalCOFI results for the wet volumes of the organisms varied widely as well, ranging from 1 to more than 300 mm^3/m^3. The CalCOFI net is of #30XXX silk gauze (mesh opening approximately 602 μ) with #56XXX silk (mesh aperture 310 μ) in the last 40 cm of the cod end. Their tows were made routinely from a depth of about 140 m to the surface, thus being deeper than most of the pump samples.

The calculated volume of the micro-zooplankton collected by the pump amounts to between 10 and 30% of the larger zooplankton volume as estimated from the CalCOFI data, with a general decrease from slope stations to oceanic sites. In considering the relative importance of the micro-zooplankton, this comparison should be considered to be approximate at best due to the necessity of using data from the CalCOFI sampling from earlier years, the size break between the lower limit of the CalCOFI net sample and the upper limit of the pumped material, the differences in depths sampled, and the presence of interstitial liquid (Ahlstrom and Thrailkill, 1963) in the CalCOFI wet volume determinations.

Data from the single plankton tow which was taken for direct comparison with pumped samples at Station III suggests that the mean volume estimates calculated from CalCOFI cruises may be considerably greater than the values

for the period currently under study. At this station a tow with the multiple serial plankton sampler developed by Longhurst et al. (1966) was made from approximately 200 m to the surface immediately after the pump sampling. The mesh of this net was 602 μ, like the CalCOFI net. The plankton volume as determined by the method of Thrailkill (1956) was 13.3 mm^3/m^3. Thus the calculated volume of the micro-zooplankton for this station, 12.0 mm^3/m^3, was 90% of that of the "Longhurst net" sample. Direct comparisons of this nature using 202-μ mesh net tows over the same depth sampled by the pump will be made during future cruises.

Food Chain Considerations

With the indication that the micro-zooplankton may be relatively abundant in different oceanic environments, their relationship to the phytoplankton and larger zooplankton as members of the marine food chain must be carefully considered. Their role as grazers of planktonic algae and, hence, in the transfer of energy between trophic levels has not been directly evaluated, but recently this has been the subject of some speculation. For example, Steemann Nielsen (1962) suggested the potential importance of these forms as an "extra link" in the food chain. Adams and Steele (1966) also suggested the grazing potential of the small zooplankton would be significant. Cushing and Vucetic (1963) counted the zooplankton collected in the North Sea with a Fine International net and a Hensen net at several times of the year and concluded that the numbers and probably biomass of small forms other than copepods and *Oikopleura* indicated that they would be relatively unimportant as grazers of the phytoplankton. They, however, did not consider the Tintinnidae, found at times in numbers greater than $1000/m^3$, since they assumed these did not eat algae. Observations in this laboratory (unpublished) on the tintinnid *Favella franciscana* Kofoid and Campbell have indicated the ready grazing of this species on a variety of phytoplankton organisms, particularly dinoflagellates. Gold (1966) has recently reported success in cultivating a tintinnid *Tintinnopsis* sp. on a diet which included several flagellates and the yeast *Saccharomyces cerevisiae*. Campbell (1926, 1927) described the food of the tintinnids *Tintinnopsis nucula* (Fol) Laackmann and *Favella franciscana* (*F. serrata*, Campbell, 1927) as consisting of bacteria, diatoms, dinoflagellates, radiolarians, and chrysomonads. Entz (1909) found, in addition, coccolithophorids and non-loricate ciliates in the diet of *Favella*.

A full knowledge of the quantitative aspects of the micro-zooplankton in food chain considerations must await physiological studies of the organisms. The major groups of organisms among the micro-zooplankton are representative of different physiological types with regard to feeding, growth, reproduction, etc., which would contribute variously to marine food chain considerations. The protozoan groups were shown to be present in relatively large numbers at the sites we sampled, but their total volume was lower than that of the metazoans. However, as small organisms have higher rates for physiological activities (e.g. respiration, Zeuthen (1947); phosphorus excretion, Johannes

(1964)) than larger forms, they may be of great interest to the overall trophodynamic picture.

Much of the available phytoplankton material in the sea is of a size which is marginally small for the efficient use by larger herbivores (see Anraku and Omori, 1963) and could be better utilized by smaller organisms, which may, in turn, be preyed upon by omnivorous and carnivorous copepods and other zooplankton. Haeckel (1887) found radiolarian skeletons in the guts of a wide range of zooplankters including siphonophores, salps, heteropods, pteropods, and various crustaceans. Also, evidence is being accumulated that zooplankters heretofore considered to be primarily herbivorous are in actuality omnivores, in some cases even having preference for animal food, much of it in the size range missed by the nets with large mesh. Anraku and Omori (1963) reported that *Calanus finmarchicus* and several other copepods feed readily on *Artemia* (brine shrimp) nauplii. *Metridia* sp. was found to eat *Artemia* nauplii in preference to six species of phytoplankton (Mullin, personal communication in Conover, 1964).

Micro-zooplankton and Mesh Size of Filter Cloth

The fact that certain animal forms, both protozoan and metazoan, passed through the 35-μ mesh aperture underlines the need for extremely fine filters to sample all zooplankton in marine communities. Even the finest mesh available will pass some of the naked protozoan forms. These are organisms which often are not recognizable in preserved samples and must be enumerated immediately in unpreserved samples.

It can be argued that the forms passing the 35-μ cloth were either forced through or passed through enlarged apertures. In determining the size of organisms to be retained by a given mesh, the measure to use is the diagonal of the mesh aperture and the smallest dimension of the organism. Theoretically, the diagonal of 35-μ mesh material should be 49.5 μ, but this was the largest diagonal measured of 87 apertures picked by us at random from a piece of *dry* Nitex nylon. The average diagonal was 43 μ. Measurements, generally length and width, of naupliar and post-naupliar copepods, tintinnids, and Foraminifera counted in the −35 samples from the three traverses taken at Station III were averaged (Table V). In general the smallest dimen-

Table V. Average dimensions (μ) of various groups of organisms in the water sample passing the 35-μ cloth at Station III, December 11, 1965. (Numbers of organisms averaged in parentheses.)

Group of organisms	Traverse		
	1	2	3
Copepoda (post-naupliar)	28 × 84 (2)	49 × 157 (4)	45 × 137 (13)
Copepoda (naupliar)	28 × 70 (1)	22 × 62 (3)	22 × 56 (4)
Tintinnidae	–	42 × 56 (1)	42 × 73 (10)
Foraminifera	39 × 50 (7)	45 × 56 (10)	45 × 56 (45)

sion measured was less than the diagonal of the mesh aperture. Even for the largest of these, only slight force, if any, would be needed to pass the organisms through the meshes considering the plasticity of their coverings, their capacity to be compressed, and/or the possible distortion of the nylon filter cloth material. Also, due to the free-fall of the water passing through the plankton collecting unit used in this work and the motion of the ship, the samples retained on the cloths were generally moved around and, thus, were given more opportunity to orient in a position to pass the mesh than with towed nets where there is continual pressure holding the organism in place.

ACKNOWLEDGMENTS

This study was supported through National Science Foundation Grant GB-3175. The cost of ship operations was provided through NSF Grant GB-4408.

The authors greatly appreciate the valuable suggestions and continued interest of Dr John D. H. Strickland throughout this study. We wish also to thank Robert E. Bower, Peter H. Wiebe, and Joe T. Hart for their help during the collecting of the plankton samples.

REFERENCES

ADAMS, J. A., AND J. H. STEELE. 1966. Shipboard experiments on the feeding of *Calanus finmarchicus* (Gunnerus). *In* H. Barnes [ed.] Some contemporary studies in marine science. p. 19–35.

AHLSTROM, E. H., AND J. THRAILKILL. 1963. Plankton volume loss with time of preservation. Rept. CalCOFI IX, July 1960–June 1962. p. 57–73.

ALLEN, W. E. 1939. Micro-copepoda in marine phytoplankton catches. Science, **89**: 532–533.

ANRAKU, M., AND M. OMORI. 1963. Preliminary survey of the relationship between the feeding habit and the structure of the mouth parts of marine copepods. Limnol. Oceanog., **8**: 116–126.

BEERS, JOHN R., GENE L. STEWART, AND JOHN D. H. STRICKLAND. 1967. A pumping system for sampling small plankton. J. Fish. Res. Bd. Canada, **24**(8): 1811–1818.

CAMPBELL, A. S. 1926. The cytology of *Tintinnopsis nucula* (Fol) Laackmann with an account of its neuromotor apparatus, division, and a new intranuclear parasite. Univ. Calif. Publ. Zool., **29**: 179–236.

1927. Studies on the marine ciliate *Favella* (Jorgensen), with special regard to the neuromotor apparatus and its role in the formation of the lorica. Ibid., **29**: 429–452.

CONOVER, R. J. 1964. Food relations and nutrition of zooplankton. Proc. Symp. Exptl. Marine Ecol., Univ. Rhode Island, Ocean. Publ., **2**: 81–91.

CUSHING, D. H., AND T. VUCETIC. 1963. Studies on a *Calanus* patch. III. The quantity of food eaten by *Calanus finmarchicus*. J. Marine Biol. Assoc. U.K., **43**: 349–371.

DUSSART, B. H. 1965. Les différentes catégories de plancton. Hydrobiologia, **26**: 72–74.

ENTZ, G., JR. 1909. Studien über Organisation und Biologie der Tintinniden. Arch. Protistenk., **15**: 93.

GOLD, K. 1966. The role of ciliates in marine ecology. I. Isolation and cultivation of a member of the Order Tintinnida. Am. Zool., **6**: 513.

HAECKEL, E. 1887. Report on the radiolaria collected by H.M.S. CHALLENGER during the years 1873–1876. Challenger Rept., Zool., **18**: 1803 p.

HANSEN, V. K., AND K. P. ANDERSEN. 1962. Sampling the smaller zooplankton. Rappt. Procés-Verbaux Réunions Conseil Perm. Intern. Exploration Mer, **153**: 39–47.

HOLMES, R. W. 1962. The preparation of marine phytoplankton for microscopic examination and enumeration on molecular filters. U.S. Fish Wildlife Serv., Spec. Sci. Rept. Fish., No. 433. 6 p.

HOLMES, R. W., AND T. M. WIDRIG. 1956. The enumeration and collection of marine phytoplankton. J. Conseil Conseil Perm. Intern. Exploration Mer, **22**: 21–32.

JOHANNES, R. E. 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. Science, **146**: 923–924.

LOHMANN, H. 1908. Untersuchungen zur Feststellung des völlstandigen Gehaltes des Meeres an Plankton. Wiss. Meeresunters., Abt. Kiel, N.F., **10**: 131–370.

LONGHURST, A. R., A. D. REITH, R. E. BOWER, AND D. L. R. SEIBERT. 1966. A new system for the collection of multiple serial plankton samples. Deep-Sea Res., **13**: 213–222.

PAASCHE, E. 1960. On the relation between primary production and standing stock of phytoplankton. J. Conseil Conseil Perm. Intern. Exploration Mer, **26**: 33–48.

STEEMANN NIELSEN, E. 1962. The relationship between phytoplankton and zooplankton in the sea. Rappt. Procés-Verbaux Réunions Conseil Perm. Intern. Exploration Mer, **153**: 178–182.

THRAILKILL, J. R. 1956. Relative areal zooplankton abundance off the Pacific coast. U.S. Fish Wildlife Serv., Spec. Sci. Rept. Fish., No. 188. 85 p.
1957. Zooplankton volumes off the Pacific coast, 1956. Ibid., No. 232. 50 p.
1959. Zooplankton volumes off the Pacific coast, 1957. Ibid., No. 326. 57 p.
1961. Zooplankton volumes off the Pacific coast, 1958. Ibid., No. 374. 70 p.
1963. Zooplankton volumes off the Pacific coast, 1959. Ibid., No. 414. 77 p.

UTERMÖHL, H. 1931. Neue Wege in der quantitativen Erfassung des Planktons. Verh. Intern. Ver. Limnol., **5**: 567–597.

ZEUTHEN, E. 1947. Body size and metabolic rate in the animal kingdom with special regard to the marine microfauna. Comp. Rend. Lab. Carlsberg, **26**: 17–161.

Migratory Behavior of Sockeye Salmon Fry and Smolts[1]

By W. L. Hartman, W. R. Heard, and B. Drucker

Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska

ABSTRACT

Considerable new data on the characteristics of sockeye fry and smolt migrations, direct underwater observations of migrating smolts, and a review of the literature are presented here with a synthesis, evaluation, and interpretation of possible survival advantages of these phenomena. Most fry migrations from spawning areas to nursery lakes take place in the spring, when harsh winter conditions in lakes are moderating and the growing season is beginning. Smolt migrations to salt water closely follow spring breakup of the ice and warming of the lake water. The time of smolt migration is correlated closely with latitude: migration is earlier in southern streams than in northern streams. The duration of seasonal migration appears to be strongly related to travel distance to the trunk river outlet. The smolt exodus is rapid and regular in single-lake systems but irregular and extended in multilake or multibasin systems. The frequency distribution of smolts migrating from two-lake or two-basin systems is usually bimodal. Most migrations commence as water temperatures near 40 F and are over when temperatures approach 50 F. Migrations of smolts and especially fry are mainly confined to the darkest hours of the night. In general, in any one season, the oldest and the largest smolts in each age-group migrate first. Other factors, such as the thickness of the ice, effectiveness of solar radiation in melting ice and warming water, and daily weather (including sunlight and wind), also influence seasonal and diel migration patterns. Underwater observations of smolts at night during migration show that they are schooled, travel in the upper water levels in shallow rivers and deeper (but not near the bottom) in deeper rivers, and usually face downstream and swim as they migrate. During migrations, fry and smolts are both often subjected to a depensatory mortality from intense predation by birds and fish. A factor disporportionately affecting different smolt populations is the length and number of restricted passages along the route to the ocean. Smolts migrating in multilake systems must encounter heavier predation than smolts migrating from single-lake systems. Predation is probably minimized en route because of innate migratory behavior patterns. Exceptions to the general migratory behavior of fry and smolts are described to show the wide range in behavioral response to variable environmental situations.

INTRODUCTION

The freshwater life history of young sockeye salmon (*Oncorhynchus nerka*) usually includes two relatively short periods of active migration: fry migrate to nursery lakes after emerging from stream, river, or lake spawning gravel; after a period that may last as long as 3 years, they leave the lakes as smolts and migrate to salt water. During these migrations the fry and smolts are confined to narrow pathways in the stream or trunk rivers. Predators congregate in and around these restricted pathways to prey on the migrants. Very likely migratory behavior with survival advantages has evolved.

Although sockeye fry are known to migrate upstream into lakes from outlet rivers (e.g. Karluk River, Alaska, and Chilko River, British Columbia

[1]Received for publication June 15, 1967.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

(Andrew and Geen, 1960)), downstream migration into lakes is more common. Certain facets of the behavior of sockeye fry migrating downstream to nursery lakes have already been reported (McDonald, 1960; Hartman et al., 1962). Briefly, the fry face downstream and swim actively rather than drift with the current, mainly during darkness, i.e. they are negatively rheotactic and phototactic. During daylight they usually seek cover along banks and in the streambed. Neave (1955) and McDonald (1960) reported similar behavior for fry of pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*).

Less information, however, is available concerning the behavior of smolts during migration. It is known that sockeye smolts migrate chiefly at night. Foerster (1937), Kerns (1961), Burgner (1962), and Hoar (1954) studied smolts and found them to be negatively phototactic but positively rheotactic, i.e. they avoid strong light and move against the current. Hartman et al. (1962) found this behavior typical for young sockeye after they schooled in the lake, and postulated that positive rheotaxis is the dominant factor that confines juvenile sockeye to lake nursery areas until transformation to smolts.

Temperature, light intensity, lake wave action, and river discharge all have been considered as external releasers for physiologically ready salmonid smolts to migrate (Baggerman, 1960). Foerster (1937) determined that the seaward migration of sockeye from Cultus Lake was correlated with air and water temperatures during the months immediately preceding migration. He also found that the numbers leaving the lake increased on bright calm days and decreased on dull cool days. Burgner (1962) also reported that the initiation and cessation of the annual spring migrations of sockeye smolts from the Wood River Lakes, Alaska, were closely related to the increase in water temperature.

This paper presents considerable new data on the characteristics of migrations of fry and smolts in many lakes in southwestern Alaska (Fig. 1) and British Columbia. We include information from direct underwater observation of sockeye behavior in the Naknek and Karluk River systems. Much unpublished material and published reports are reviewed. All information is synthesized into a comprehensive examination of migratory behavior, and the possible survival advantages of migratory behavior are discussed.

METHODS

Material on the timing, number, age, and size composition of smolts migrating from important sockeye-producing systems in southwestern Alaska was obtained from unpublished and published reports by the Bureau of Commercial Fisheries, the Fisheries Research Institute of the University of Washington, and the Alaska Department of Fish and Game. Material on fry migratory behavior in certain tributaries at Brooks and Karluk Lakes was obtained by the Bureau of Commercial Fisheries.

Data on rheotactic responses, schooling behavior, and stream depth preference of migrating smolts were obtained by direct underwater observations by biologists wearing neoprene rubber suits. Observations were made

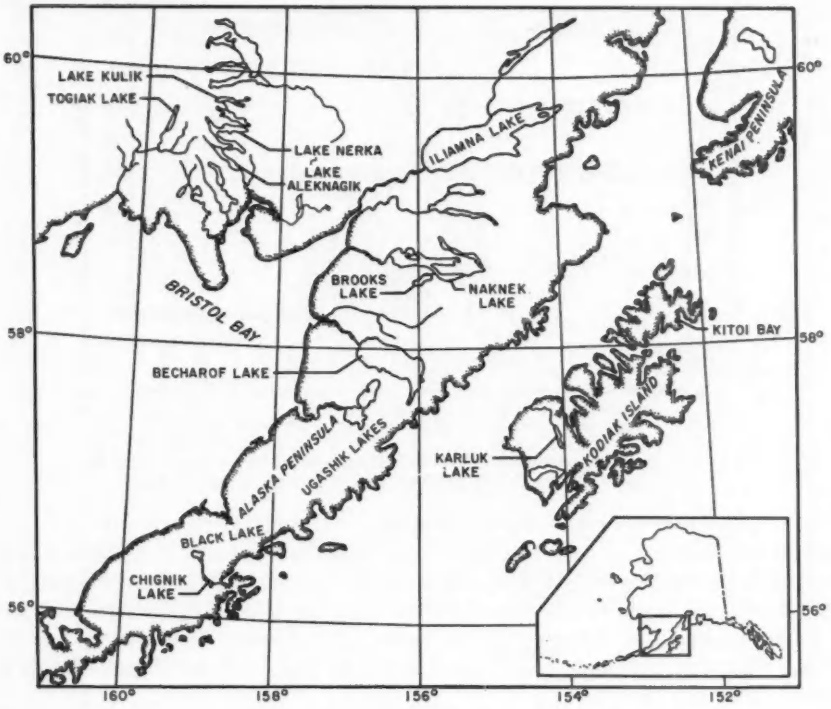

FIG. 1. Sockeye salmon nursery lakes in southwestern Alaska.

during late twilight, when sufficient light remained for observation, and during darkness, with underwater hand lamps. Sometimes lamps were turned on only at intervals for spot checking; at other times they were operated constantly. Underwater observations were made in Brooks, Grosvenor, Coville, and Naknek Rivers of the Naknek system and Karluk River of the Karluk system. The diversity of these environments permitted observations in a variety of water depths, velocities, and turbidities.

SEASONAL MIGRATIONS OF FRY AND SMOLTS

FRY

Data on sockeye fry migrations from stream spawning areas to nursery areas in Brooks and Karluk lakes have been collected for a number of years.

The seasonal migration of fry from Hidden Creek, a tributary to Brooks Lake, did not deviate significantly in 1961–64 from that of 1960, described by Hartman et al. (1962). Migrations start in late April, reach their midpoint around May 13, and are essentially completed by about May 25 (Fig. 2). Although spawning takes place during early August in both Hidden Creek

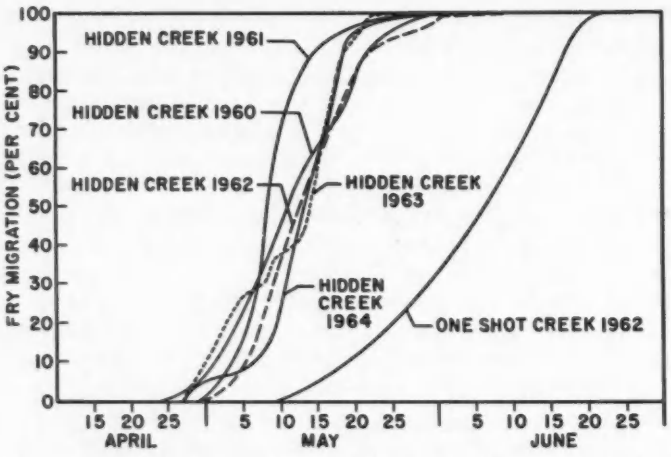

FIG. 2. Cumulative seasonal migration of sockeye fry in per cent to Brooks Lake from Hidden Creek (1960–64) and One Shot Creek (1962).

and One Shot Creek (another tributary to Brooks Lake), the peak of fry migration from One Shot Creek was more than 3 weeks later in the spring of 1962 (Fig. 2). Some of the water in One Shot Creek is from springs, and the stream is often 2 or 3 C colder in mid- and late summer than Hidden Creek. This difference evidently results in slower embryological development and a later departure of fry.

The seasonal appearance of adult sockeye returning to Karluk Lake to spawn is bimodal (Barnaby, 1944). Small lateral tributary streams receive only summer spawners; lake-beach spawning areas receive only fall spawners; and terminal tributary streams receive both summer and fall spawners.

Fry migrations from the tributaries of Karluk Lake that are seeded by summer spawners, such as Grassy Point Creek and Upper Thumb River, begin about 2 weeks earlier, on the average, than migrations at Brooks Lake (Fig. 2, 3). This difference may be due to Karluk Lake's more southerly latitude and the likelihood of earlier warming each spring.

Spawning normally occurs in both summer and fall in Canyon Creek and Meadow Creek, and the fry emerge in separate early spring and late spring migrations (Fig. 4). About 60 days separate the midpoints of the two spawning periods and the two spring migrations of fry. The timing of the early spring migration at Meadow Creek in 1962 was strikingly different from that in 1963 (Fig. 4) and also different from the six other early spring migrations observed in tributaries of Karluk Lake (Fig. 3, 4). In 1963, 50% had migrated from Meadow Creek by May 3 which is normal timing. Yet in 1962 the midpoint date was May 24. The most reasonable explanation for the difference is that water temperatures during the 1961–62 incubation period at Meadow Creek were abnormally cold.

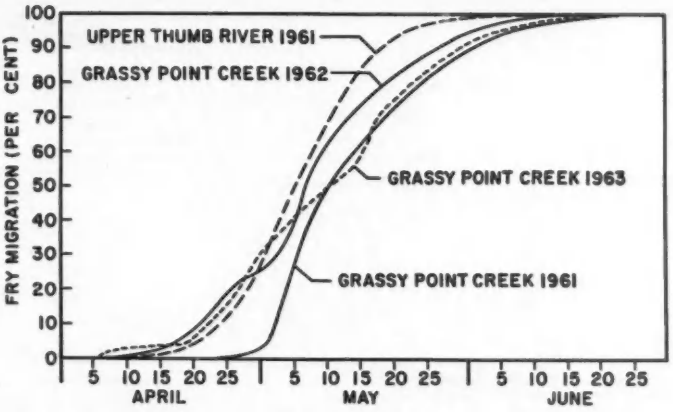

FIG. 3. Cumulative seasonal migration of sockeye fry in per cent to Karluk Lake from Grassy Point Creek (1961–63) and Upper Thumb River (1961). These fry are progeny of summer spawners.

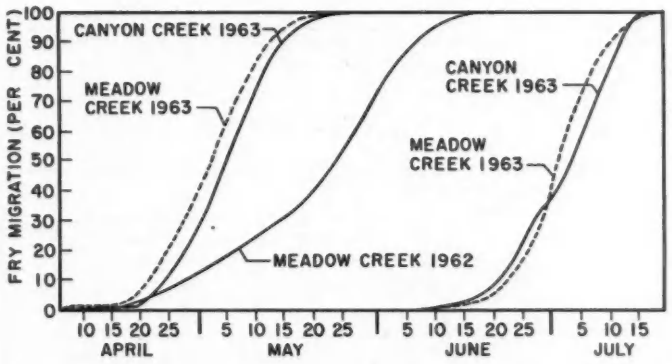

FIG. 4. Cumulative seasonal migration of sockeye fry in per cent to Karluk Lake from Meadow Creek (1962–63) and Canyon Creek (1963). These fry are progeny of both summer and fall spawners.

SMOLTS

Seasonal migrations of sockeye smolts differ considerably among the lake systems but are usually fairly consistent from year to year within each system. Smolts migrate at Cultus Lake in late April (Foerster, 1937; see Fig. 5) and in late June and early July at Lake Tazlina on the Copper River (Thompson, MS, 1964). Lakes in which migration occurs on dates between these extremes are: Lakelse Lake (Fig. 6), Chignik Lake (Fig. 7), Karluk Lake (Fig. 8), Ugashik Lake (Fig. 9), Becharof Lake (Fig. 10), Brooks Lake (Fig. 11), Naknek Lake (Fig. 12), Iliamna Lake (Fig. 13), and Lake Aleknagik (Fig. 14). The spacing along the abscissal scales is identical in Fig. 5–14, but

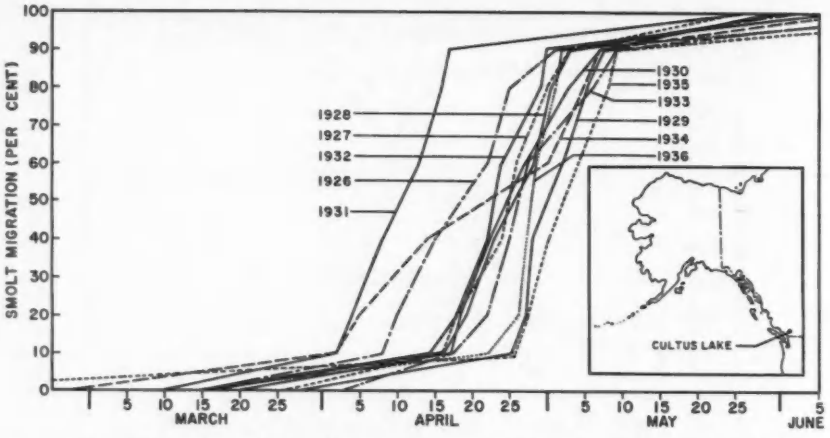

FIG. 5. Cumulative seasonal migration of sockeye smolts in per cent from Cultus Lake for 1926–36 (after Foerster, 1937).

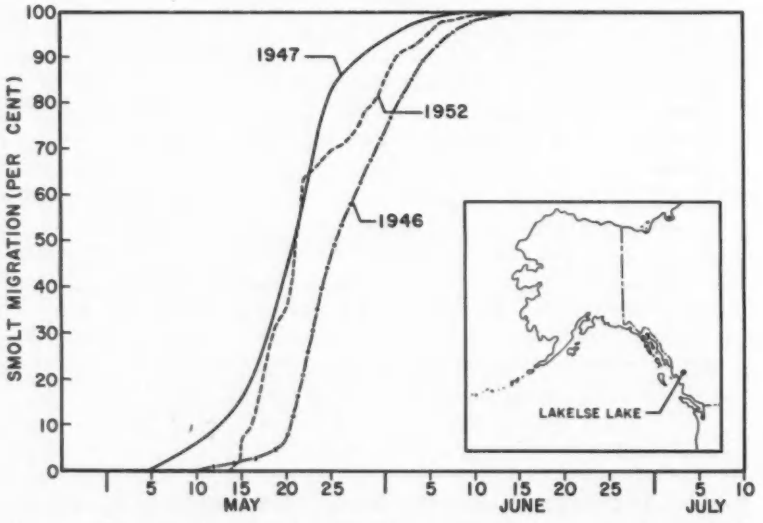

FIG. 6. Cumulative seasonal migration of sockeye smolts in per cent from Lakelse Lake (data for 1946–47 from Brett and McConnell (1950), and for 1952 from Foerster (1952)).

different calendar periods are shown on each, according to the timing of migration.

The average seasonal timing of migrations in 16 sockeye-producing systems examined (Table I, Fig. 15) shows a strikingly close correlation with

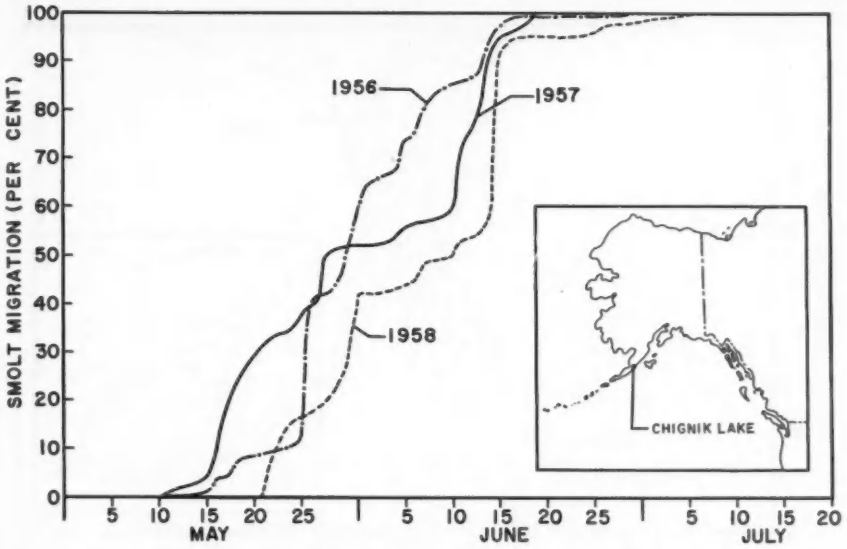

FIG. 7. Cumulative seasonal migration of sockeye smolts in per cent from Chignik Lake (after Roos, 1958, 1959).

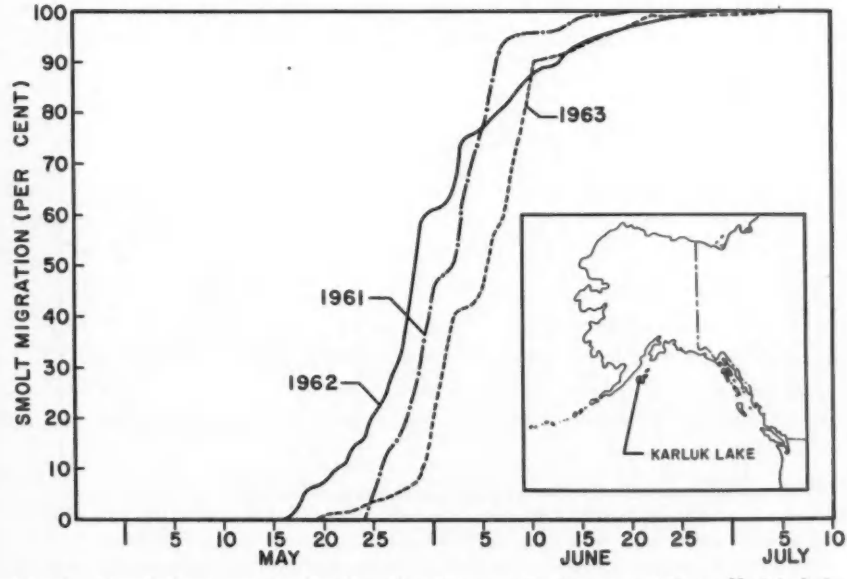

FIG. 8. Cumulative seasonal migration of sockeye smolts in per cent from Karluk Lake.

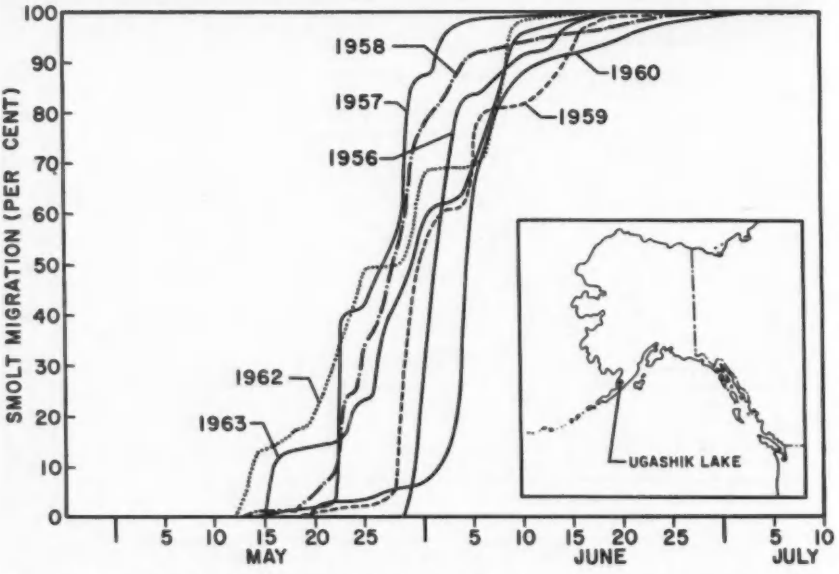

FIG. 9. Cumulative seasonal migration of sockeye smolts in per cent from Ugashik Lake.

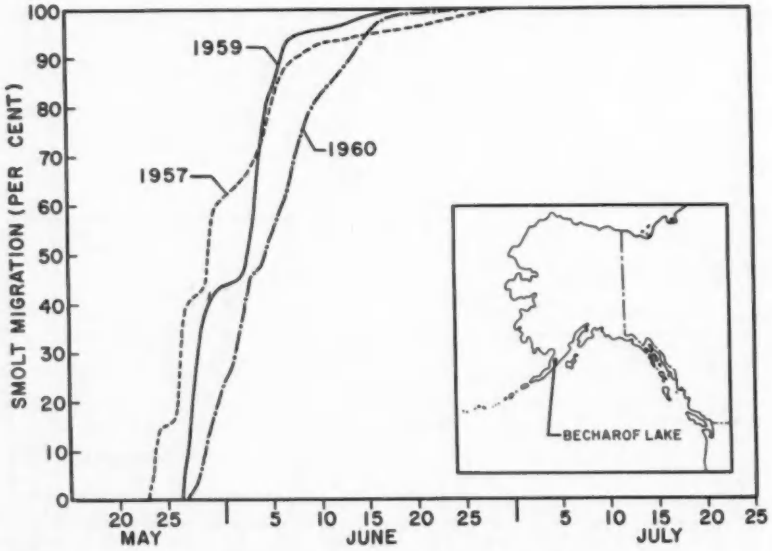

FIG. 10. Cumulative seasonal migration of sockeye smolts in per cent from Becharof Lake.

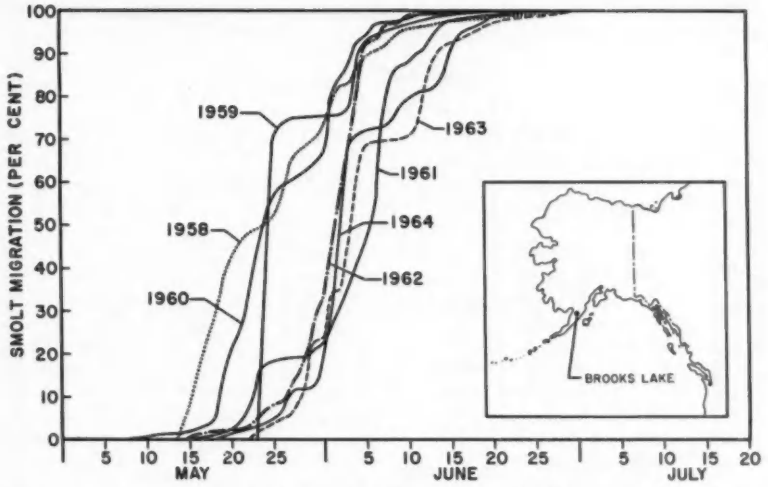

FIG. 11. Cumulative seasonal migration of sockeye smolts in per cent from Brooks Lake.

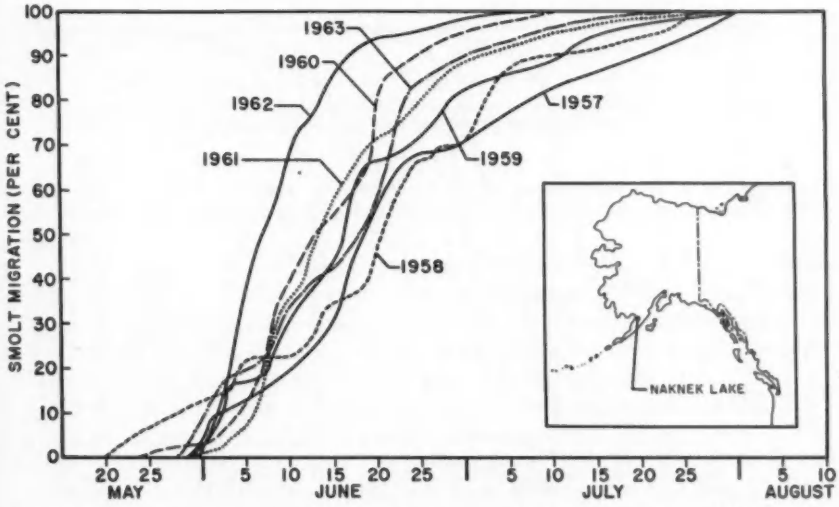

FIG. 12. Cumulative seasonal migration of sockeye smolts in per cent from Naknek Lake.

latitude (Fig. 16). Migrations occur progressively later in the season as the distance north from Cultus Lake, British Columbia, increases. The seasonal pattern for the Bolshaya River, on the western side of Kamchatka Peninsula (Semko, 1954), also fits the relationship shown by migrations in North American streams.

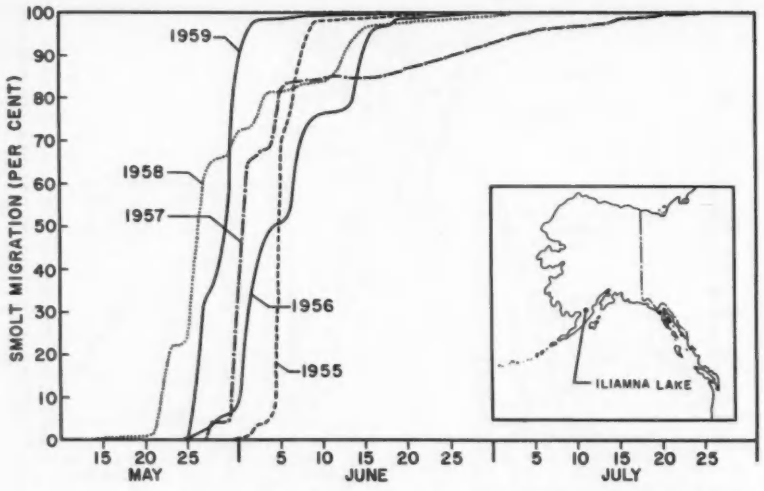

FIG. 13. Cumulative seasonal migration of sockeye smolts in per cent from Iliamna Lake (after Kerns, 1961).

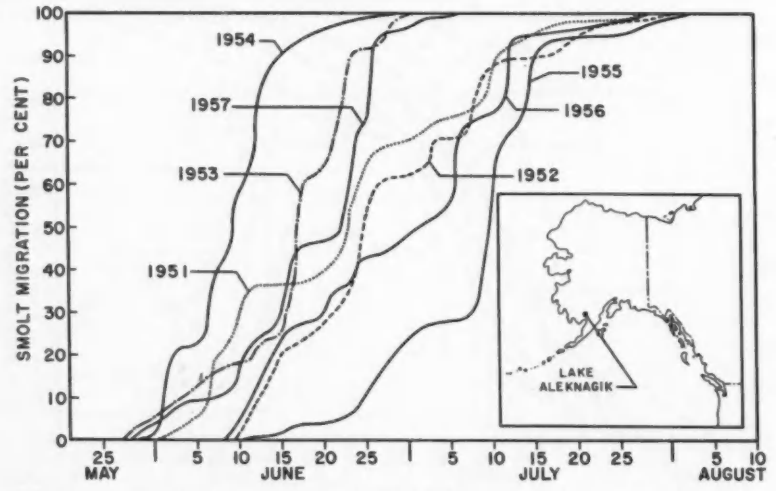

FIG. 14. Cumulative seasonal migration of sockeye smolts in per cent from Lake Aleknagik (after Burgner, 1962a).

Several authors (e.g. Chamberlain, 1907; Foerster, 1937; Burgner, 1962) have mentioned the relationship between ice breakup, warming of water temperatures, and initiation of smolt migration. Progressively increasing solar radiation in the spring in the Northern Hemisphere obviously bears

TABLE I. Average dates by which 50% of sockeye smolts have left lake systems.

Lake system	N latitude	Date[a]	No. of years of observation	Source
Cultus	49° 0′	April 25	11	Foerster (1937)
Bolshaya River	52°15′	May 12	Several	Semko (1954)
Lakelse	54°32′	May 23	3	Foerster (1952), Brett and McConnell (1950)
Babine[b]	54°50′			
Early		May 13	6	Anon. (MS, 1964)
Late		June 4	13	Anon. (MS, 1964)
Chignik	56°16′	June 3	3	Roos (1958)
Karluk	57°20′	June 3	3	Present paper
Lower Ugashik	57°35′	May 30	6	Jaenicke (MS, 1963)
Becharof	57°55′	June 1	3	Jaenicke (MS, 1963)
Kitoi	58°15′	June 5	9	Meehan (MS, 1964)
Ruth	58°15′	June 14	6	Meehan (MS, 1964)
Auke	58°23′	May 28	2	D. T. Hoopes (personal communication)
Brooks	58°28′	May 31	7	Present paper
Naknek	58°39′	June 16	7	Jaenicke (MS, 1963)
Iliamna	59°30′	June 2	9	Kerns (1961) and personnal communication
Aleknagik	59°35′	June 22	7	Burgner (1962)
Tazlina	61°55′	July 1	Several	Thompson (MS, 1964)

[a]Actual average midpoint of migration where known, or best estimate from source.
[b]Dates given for distinct early and late smolt migrations.

directly on ice breakup and warming of the water (and, in turn, on smolt migration).

Local climate and characteristics of individual lakes could account for minor deviations from the general relation between latitude and migration timing. For example, the seasonal migration at Iliamna Lake is relatively early for its latitude (Fig. 15). O. E. Kerns (personal communication) suggested that the ice cover on Iliamna Lake, the largest lake in Alaska, is relatively unstable because it often is not formed completely until mid-December. Spring winds with long fetches usually cause a rapid breakup — often in only 3 or 4 days. As a result, migrations begin relatively earlier here than in such nearby lakes as Naknek, Ugashik, and Aleknagik, where freezeup is earlier, ice is more stable, and winds are not as effective in breaking up the ice.

The seasonal migration in single-lake and multilake or multibasin systems appears strongly related to travel distance to the trunk river outlet. For single-lake systems the smolt exodus is speedy. The slopes of the curves depicting the progress of migration are steep for such lakes as Cultus (Fig. 5), Lakelse (Fig. 6), Karluk (Fig. 8), Becharof (Fig. 10), Brooks (Fig. 11), and Iliamna (Fig. 13). In any one year most of the migration occurs in a few days.

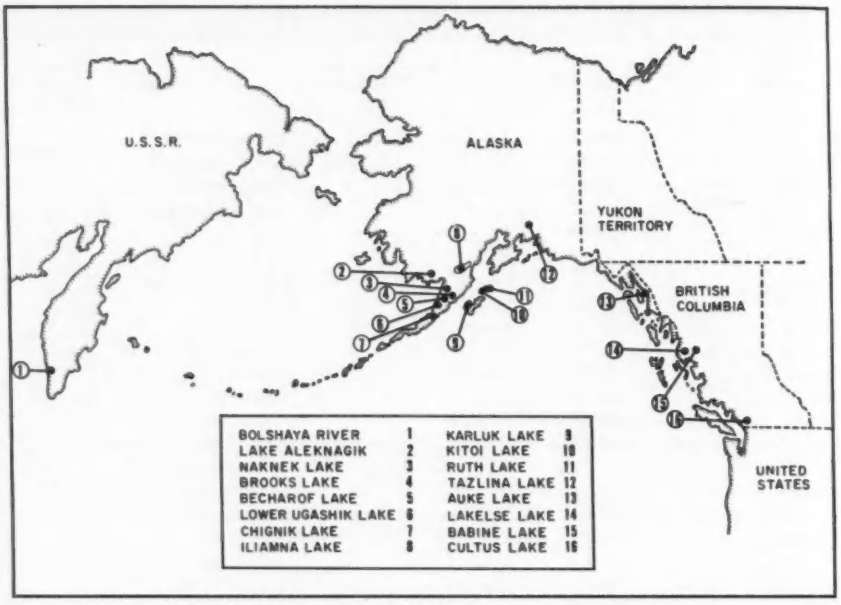

FIG. 15. Sockeye salmon-producing systems treated in analysis of the seasonal timing of sockeye smolt migrations.

For multibasin systems it seems logical that the exodus of smolts would extend over a longer period of time. The migration curves from Naknek Lake (Fig. 12) and Lake Aleknagik (Fig. 14) show an extended period of migration. These lake outlets are trunk rivers for multilake systems, and the migration is extremely irregular — a result of variations in timing of the migrations from each lake and in magnitude of the different smolt populations. Burgner (1962) concluded from seasonal changes in length-frequency distribution of smolts that the first migrants were from the lowest lake in the Wood River system, Lake Aleknagik, and that the later migrants were from the upper lakes and had been delayed by travel distances.

Johnson and Groot (1963) reported two peaks in the migration from Babine Lake (Fig. 16). Groot (1965) shows this for 4 years of data. They assumed that the migrations began throughout this multibasin system at the same time. If so, their data on tag recovery and speed of migration suggest that the first migration peak represented smolt populations from the vicinity of the outlet, consisting of Nilkitkwa Lake and the North Arm of Babine Lake; and the second migration peak represented smolts from the more distant region, the main basins of Babine Lake. The average date between these two peaks was May 24 and fell almost perfectly in line in the relation to latitude (Fig. 16).

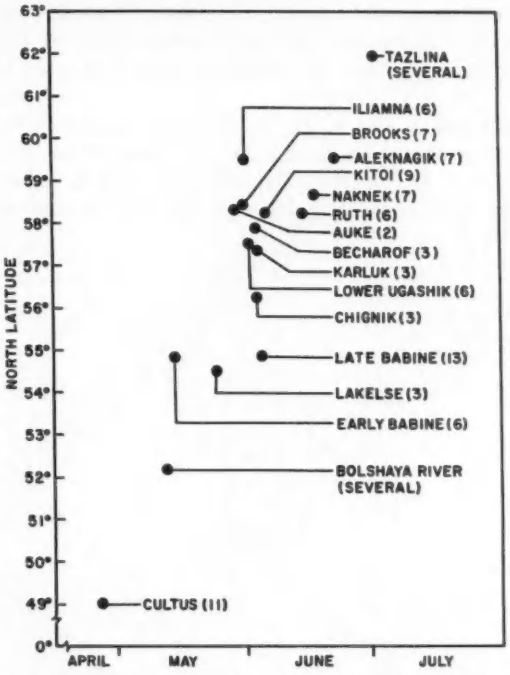

FIG. 16. Average date by which 50% of the spring sockeye smolts had migrated from lake systems located at different latitudes. Numbers in parentheses show number of years of observation.

Travel distance may not be the only cause of bimodal migrations from multilake or multibasin systems. Other important factors such as age and size of smolts and the tendency for older and larger smolts to migrate first (see section under heading "Biological and Physical Factors Associated with Smolt Migrations") must also be considered.

The two-lake Chignik system appears to have a bimodal migration. Bimodality was especially evident in 1957 and 1958 at the trunk river outlet from Chignik Lake (Fig. 7). Studies of age and length-frequency distributions and scale characteristics of the smolts (Roos, MS, 1958; Narver, MS, 1963) showed that usually the early migrants are 2 years old and are from Chignik, the lower lake; and the later migrants are 1 year old and are from Black, the upper lake.

DIEL MIGRATIONS OF FRY AND SMOLTS

FRY

Sockeye fry emerge from the gravel primarily at night (Heard, 1964) and migrate primarily at night (McDonald, 1960; Hartman et al., 1962).

We observed the seasonal diel migration patterns of sockeye fry from various tributaries for 6 years at Brooks Lake and 5 years at Karluk Lake, and present here data from four migrations that illustrate these and other related phenomena.

The observations at Brooks Lake, where fry counts were made hourly, showed clearly that nearly all migration was confined to the hours between 2100 and 0200 (Fig. 17, 18). At Karluk Lake, where counts were usually made at 2-hr intervals starting at 1900 hours early in the season and 2000

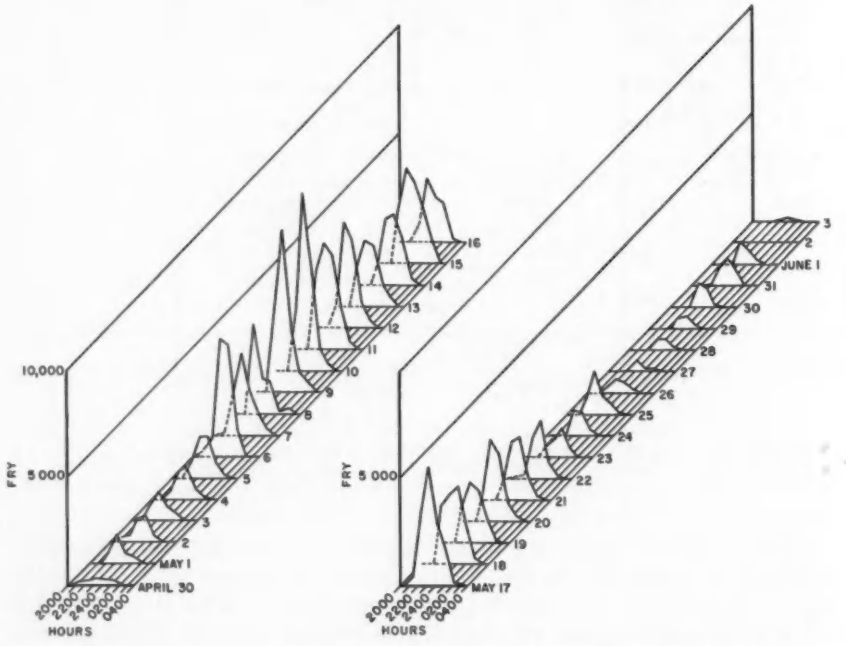

FIG. 17. Migration of sockeye salmon fry from Hidden Creek to Brooks Lake during the nights, April 30–June 3, 1962.

hours later in the season, the bulk of the migration occurred before 2400 (Fig. 19, 20). Migration started nearly an hour earlier at Karluk Lake than at Brooks Lake on the same dates. Karluk Lake is 1.5 degrees of longitude east of Brooks Lake, but this accounts for only a difference of about 6 min in time of sunset. A possible explanation for the hour's difference is that all creeks studied at Karluk Lake enter on the west side, where a high ridge of mountains blocks sunlight during the early evening. The creeks at Brooks Lake are on the northeast side of the lake and are fully exposed to sunlight later into the evening.

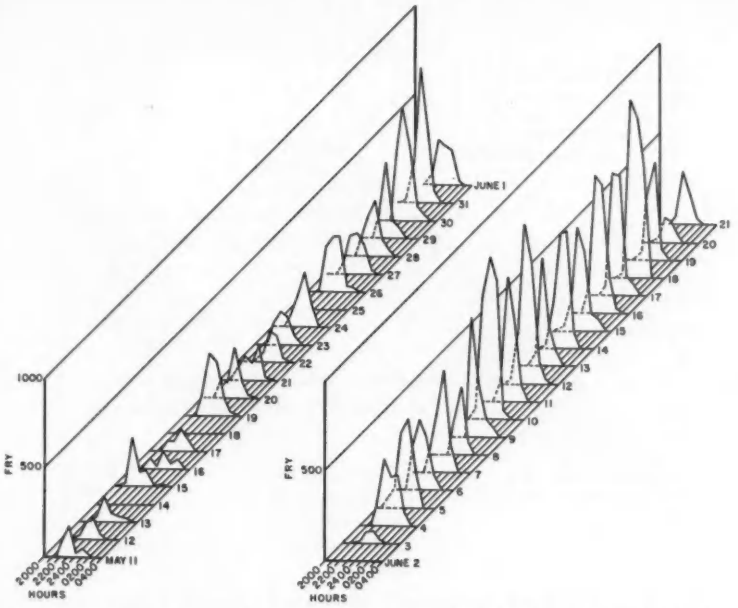

FIG. 18. Migration of sockeye salmon fry from One Shot Creek to Brooks Lake during the nights May 11–June 21, 1962.

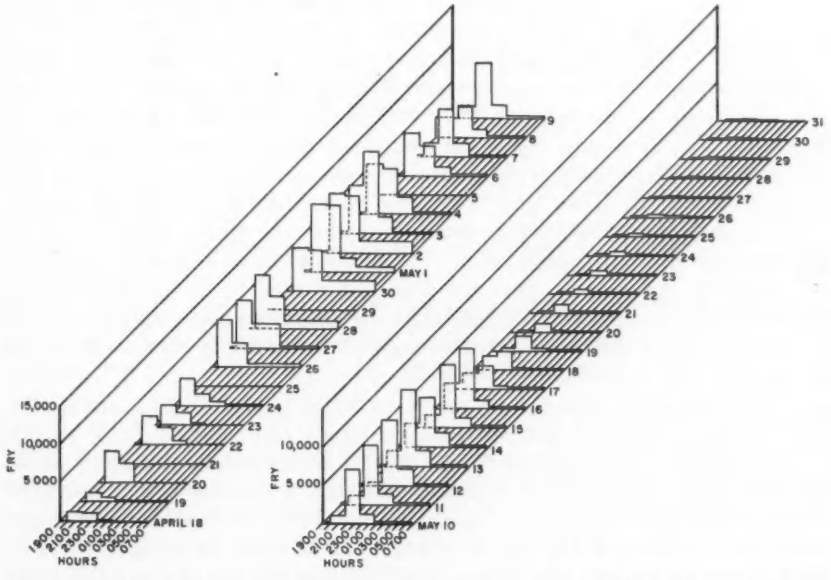

FIG. 19. Migration of sockeye salmon fry from Canyon Creek to Karluk Lake during the nights, April 18–May 31, 1963.

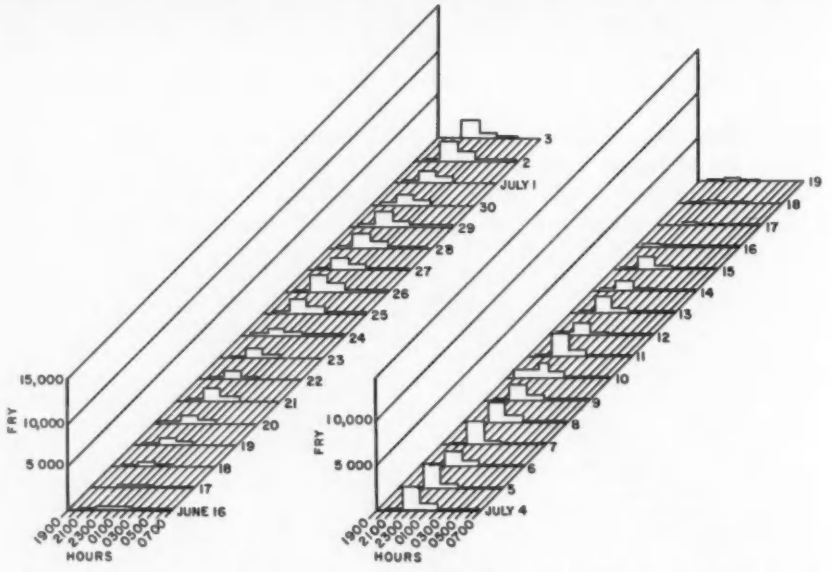

FIG. 20. Migration of sockeye salmon fry from Canyon Creek to Karluk Lake during the nights, June 16–July 19, 1963.

Another phenomenon evident for all observations on fry migrations, and also observed by McDonald (1960) and Hartman et al. (1962), is the shortening of the daily migration period and its shift to later hours as the season progresses and dusk comes later and dawn earlier. The clearest example was at Canyon Creek in 1963. The 1963 spring migration of fry produced from spawning in the summer of 1962 extended over a number of hours during late April and early May, and the peak of nightly migrations was about 2100 hours (Fig. 19). By late May the period of nightly migration was shorter, and the peak shifted to 2200 or later. The 1963 late spring migration of fry produced by spawning in the fall of 1962 continued to show the shorter period of migration, and by late June the peak had shifted to about 2300 hr (Fig. 20). Substantial migrations did not extend far enough past the summer solstice to show if nightly migration periods lengthened or peaks shifted back toward an earlier hour as daylight decreased.

SMOLTS

Most Bristol Bay sockeye smolts migrate from their lake systems during the darkest hours, 2000–0400 (Fig. 21). Only about 4% of the total migration occurs during other hours. At Karluk Lake in 1963 about 96% of the smolts migrated between 2000 and 0300 hours, and in 1964 about 92% migrated during these hours. Nocturnal migration is also the general rule at Lake Aleknagik where Burgner (1962) found that 95% of the smolts caught during 17 days

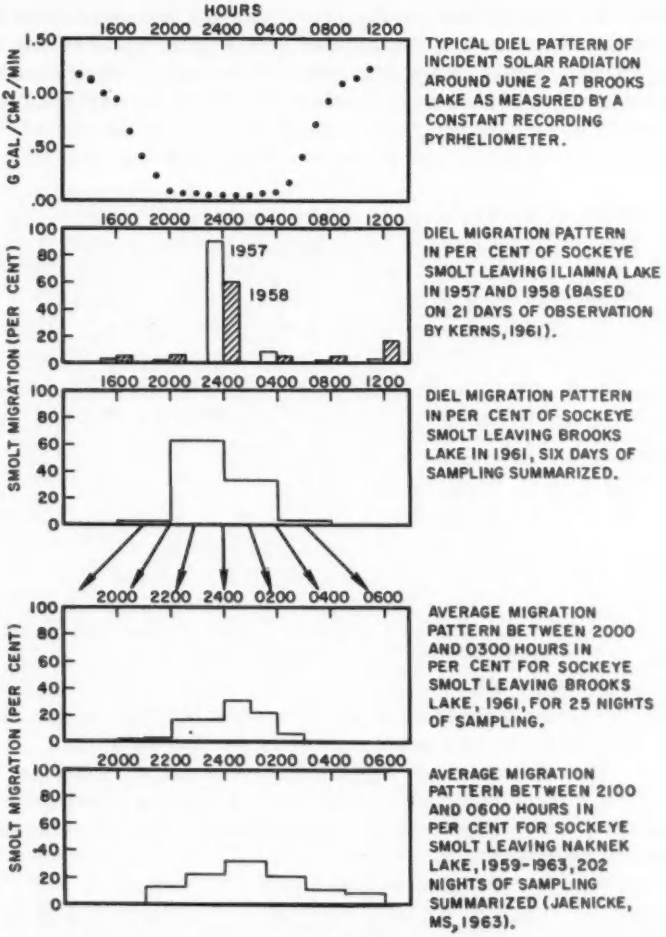
HOURS
1600 2000 2400 0400 0800 1200
G CAL/CM²/MIN
1.50
1.00
.50
.00
TYPICAL DIEL PATTERN OF INCIDENT SOLAR RADIATION AROUND JUNE 2 AT BROOKS LAKE AS MEASURED BY A CONSTANT RECORDING PYRHELIOMETER.
SMOLT MIGRATION (PER CENT)
100
80
60
40
20
0
1957
1958
DIEL MIGRATION PATTERN IN PER CENT OF SOCKEYE SMOLT LEAVING ILIAMNA LAKE IN 1957 AND 1958 (BASED ON 21 DAYS OF OBSERVATION BY KERNS, 1961).
DIEL MIGRATION PATTERN IN PER CENT OF SOCKEYE SMOLT LEAVING BROOKS LAKE IN 1961, SIX DAYS OF SAMPLING SUMMARIZED.
2000 2200 2400 0200 0400 0600
AVERAGE MIGRATION PATTERN BETWEEN 2000 AND 0300 HOURS IN PER CENT FOR SOCKEYE SMOLT LEAVING BROOKS LAKE, 1961, FOR 25 NIGHTS OF SAMPLING.
AVERAGE MIGRATION PATTERN BETWEEN 2100 AND 0600 HOURS IN PER CENT FOR SOCKEYE SMOLT LEAVING NAKNEK LAKE, 1959-1963, 202 NIGHTS OF SAMPLING SUMMARIZED (JAENICKE, MS, 1963).

FIG. 21. Diel patterns of solar radiation at Brooks Lake, diel sockeye smolt migration at Iliamna Lake and Brooks Lake, and nocturnal smolt migration pattern at Brooks and Naknek lakes.

of round-the-clock fishing in 1951 were taken between 2100 and 0200 hours. Groot (1965) presents data for 6 days for smolt migrations from Great Central Lake in British Columbia in 1960. Migrations began after sunset and were confined mainly to the period 2000–2400 hr. Kerns (1961) observed similar behavior in 1957 at the outlet to Iliamna Lake (Fig. 21) when 91% of the migration took place between 2200 and 0200 hr. He found, however, during 1958, when the migration was extremely heavy, that about 38% of the smolts caught in 9 days of round-the-clock fishing were taken between 0200 and

2200 hours. Kerns suggested that carryover of the migration into daylight hours was directly related to the number of migrants. Possibly the capacity of the outlet stream to accommodate migrants during darkness was exceeded. H. W. Jaenicke (personal communication) suggested that daylight migrations of smolts such as he observed at Naknek River may also be related to heavy fog, cloudbursts, or heavy onshore winds that cause high turbidity in the outlet.

The peaks of nocturnal smolt migration in the latitude of the Alaska Peninsula generally are around midnight. Nocturnal migration of smolts at Brooks and Naknek Lakes is greatest between 2300 and 0200 hr (Fig. 21). The peaks vary with seasonal and daily changes in light. In 1957 and 1958, when the migration from Iliamna Lake took place in May (Kerns, 1961), darkness set in around 2200 hr, and the peak migration was between 2200 and 2300 hr. In 1955 and 1956, when the migration took place chiefly in early June, darkness set in around 2300 hr and the peak migration was between 2300 and 2400 hr. Farther south on the Alaska Peninsula at Chignik Lake, Thorsteinson and Roos (MS, 1958) detected a shift in peak of migration from 2300 to 2400 hr as the season progressed. They also noted a tendency for the evening migration peak to occur earlier on dark, overcast days.

The timing of the peak migration from Naknek Lake (Fig. 21) was usually later in the evening than at Brooks Lake, Iliamna Lake, Lake Aleknagik, or Chignik Lake. Smolts were sampled in the outlet near the lake, except at Iliamna Lake, where smolts were sampled about 2 miles downstream from the lakes, and at Naknek Lake, where smolts were sampled about 8 miles downstream from the lake. Presumably smolts migrated from Naknek Lake during the first hours of darkness as at other lakes, but the distance of 8 miles from the lake outlet to the sampling site caused the later peak.

H. W. Jaenicke (personal communication) has observed at Naknek River that after the summer solstice on June 21, and especially by mid- and late July, the peak of migration shifts to an earlier hour as darkness comes earlier in the evening.

BIOLOGICAL AND PHYSICAL FACTORS ASSOCIATED WITH SMOLT MIGRATIONS

A number of biological and physical factors have been related by other scientists to seasonal and diel migration of smolts. Among them have been age structure of the smolt population, solar radiation, water temperature, ice breakup, wind intensity and direction, cloud cover, rainfall, and water level. Certain important points are briefly reviewed below, including our recent evidence on the significance of some of these relations.

Smolt Size and Age

Usually the older sockeye smolts and the largest in each age-group migrate first in the spring (Foerster, 1937; Barnaby, 1944; and Krogius and Krokhin, 1948). Thorsteinson and Roos (MS, 1958) found at Chignik Lake that the

largest smolts migrated earliest in the season and earliest in the evening. Burgner (1962) observed at Lake Aleknagik that the largest smolts also migrated first in the evening, and O. E. Kerns (personal communication) reported that at Iliamna Lake the oldest smolts migrated earliest in the season and earliest in the evening.

Migration Stimulation

Time of ice breakup, spring overturn, and warming of the water are related to the amount of solar radiation and the thickness of the ice cover. The start of smolt migrations has been related to time of ice breakup for Lake Aleknagik (Burgner, 1962), for Iliamna Lake (Kerns, 1961), and for Kitoi Lake (Parker and Vincent, 1956). However, the shift in young sockeye from a nonmigratory to a migratory stage of their life cycle may be related strongly to photoperiodism. So the timing of migration may not deviate as much from calendar dates as it would were it strongly related only to climatic conditions.

In lakes that do not freeze over, the migration stimulus still appears to relate strongly to rising spring water temperatures. Foerster (1937) found that migration began at Cultus Lake as temperatures rose past 40 F. In 1934 the minimum winter water temperatures did not drop below 41 F, however, and yet the smolts did not migrate before early spring; in 1936 winter water temperatures fell as low as 37 F (March 2) yet migration occurred about the same time as in 1934. So, although slight increases in water temperatures in mid-March some years were followed by initiation of smolt migrations, the migrations also occurred in other years lacking the thermal stimulus immediately before the migrations, and we must again turn to photoperiodism as the overriding stimulus or releaser.

Thermal Range

During 6 years of observations at Brooks Lake and 3 years at Karluk Lake, we found that smolt migrations began in strength as spring water temperatures rose above 40 F and were essentially over as temperatures rose past 46 F. Sudden decreases in water temperatures would be accompanied by lulls in the migration, after which sudden increases in temperatures would correspond with surges in the migration. These general phenomena are illustrated in data from Brooks Lake (Fig. 22) for 1961.

Water temperature ranges within which most smolt migrate are not materially different in other areas. In Cultus Lake (Foerster, 1937) and Lake Aleknagik (Burgner, 1962), spring smolt migrations started as lake water temperatures rose above 40 F and stopped as they rose above 49 F. Parker and Vincent (1956) found the temperature range for migration at Kitoi Lake to be 40–55 F. At Chilko Lake in British Columbia migrations started at about 38 F and were nearly over when temperatures reached 45 F (Harvey, 1963). Jaenicke (MS, 1963) found that most smolts left Ugashik Lake when water temperature ranged between 39 and 46 F.

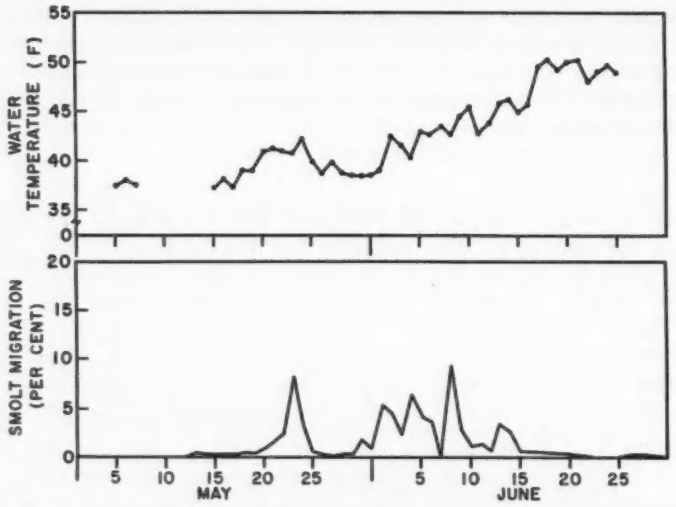

FIG. 22. Mean water temperatures and percentage of the season's total smolt migration from Brooks Lake on different dates between May 5 and June 28, 1961.

OTHER FACTORS

Varying wind, cloud cover, rainfall, and water levels have been suggested as causing fluctuations in the intensity of migration. Thorsteinson and Roos (MS, 1958) noted that smolt catches in Chignik River were small when winds were offshore at the lake outlet, but large when winds were onshore. Jaenicke (MS, 1963) also observed this phenomenon at Ugashik and Becharof lakes. At Karluk Lake, too, wind onshore at the outlet usually was coincident with large outmigrations.

A number of factors may be operating when the wind is onshore. Surface currents move onshore, and warmer surface waters may "pile up" at the outlet; as a result, temperature in the outlet stream may rise slightly, and turbidity usually increases. It is not known which of these factors affect the intensity of migration. Hartman et al. (MS, 1961) found that a strong onshore wind at Brooks Lake not only greatly accelerated the intensity of the smolt migration but also greatly altered the horizontal distribution of smolts in Brooks River below the lake outlet. Smolts were concentrated in an onshore current of turbid water caused by the direction of the wind in relation to the location of the outlet. Smolts remained in the turbid band of water in the river for a sufficient distance to materially alter the pattern of catches in fyke nets 100 yards downstream from the lake.

Considering factors other than wind, Foerster (1937) observed at Cultus Lake that daily smolt migrations increased after warm bright days and decreased after cool dull days.

BEHAVIOR OF MIGRATING SMOLTS

Our underwater observations on smolt behavior were made with three questions in mind. Do smolts migrate individually or in schools? At what water depth do smolts migrate? Are smolts passively displaced downstream during migration, or do they usually migrate facing downstream and actively swimming?

School Behavior

Observations at several locations revealed that sockeye smolts schooled during migration. At Brooks River, only 15 smolts were seen migrating individually, whereas 25 schools of 2–10 smolts, 22 schools of 11–100, and 20–30 schools of more than 100 smolts were seen migrating. On two occasions in 1962 at Karluk many schools of 400–800 migrating smolts were seen. In 1963 at Karluk Lake, the size of schools ranged from 25 to 300 (eight observations). During extremely heavy migrations in 1962 at Naknek River, thousands of smolts were observed migrating in a continuous band. Very possibly these schools were so close together that they coalesced. The size of schools of sockeye smolts at Lakelse Lake usually varied between 20 and 200 (Brett and Alderdice, 1958).

Underwater observations at Karluk and Brooks Lakes indicated that smolts are schooled in the lake near the outlets. Other observers have reported smolts schooled as they approach lake outlets at the time of migration, e.g. Foerster and Ricker (1953) at Cultus Lake, Burgner (1962) at Lake Aleknagik, Johnson and Groot (1963) at Babine Lake, R. L. Wallace (personal communication) at Coville Lake, and C. J. DiCostanzo (personal communication) at Ualik and Ugashik lakes.

Migrating schools of smolts approaching Brooks Lake outlet generally have an ovoid shape. As the school enters fast current in the outlet (2–4 ft/sec), it becomes elongated and narrower. Surface "bow waves" from ovoid schools of young-of-the-year migrants leaving Coville Lake were observed by us on calm days throughout August 1962.

Depth of Travel

In the clear-water rivers draining Brooks and Coville Lakes, sockeye smolts migrate in the upper layer of water. In 37 schools of smolts migrating from Brooks Lake (Fig. 23), most smolts were in the top 20% of water depth and none were in the bottom 20%. Most smolts in the top tenth of the water column were at least several inches from the surface. Two small schools were observed in the 0–20% range in the outlet to Coville Lake, where the water averaged 6.5 ft deep. In the outlet to Naknek Lake, a steady stream of migrating smolts was seen between 2.5 and 3.5 ft (stream depth slightly more than 5 ft), or in the layer of water between 50 and 75% of the distance from the surface. O. E. Kerns (personal communication) has observed that smolts migrate in Kvichak River near the surface during darkness and near the bottom in the deepest channels during daylight.

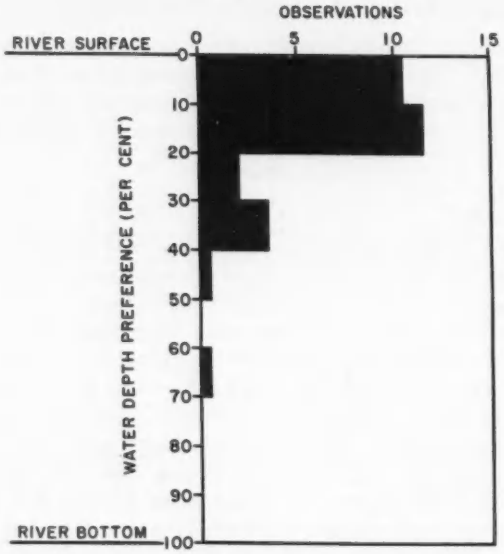

FIG. 23. Sockeye smolt schools migrating at different water depths in the outlet of Brooks Lake, 1961–63. Average depth of each school is plotted in the appropriate tenth of the distance from the surface to the bottom. The figure is based on observations of 37 schools representing several thousand smolts.

These observations seem to agree with Stuart's (1962) findings on the importance of visual contact with stream bottoms to migrating salmonid smolts. He demonstrated experimentally that the fish strive to remain at a certain relevant distance from the bottom, depending on turbidity and fish size. This distance is shortened by increased turbidity and extended by increased fish size. Thus, in the deeper more turbid streams, such as Naknek River, smolts would be relatively farther from the surface than in the shallower clear streams like the outlet to Brooks Lake. Although smolts moving toward the outlet of Karluk Lake in 1962 and 1963 were in schools at depths between 10 inches and 7 ft, definite preference for the littoral shallow areas was obvious.

A series of observations at the outlet of Coville River on August 20, 1962, may bear on the role of visual contact with the stream bottom during migration. A steady procession of schools of young-of-the-year sockeye was observed approaching the lake outlet along the northeast shoreline between 1500 and 1700 hr. Bow waves of these schools could be seen easily on the calm surface by an observer on shore. At the point where these schools passed from the lake into the river, the depth increases sharply from less than 2 ft to about 5 ft. Underwater observations indicated that as schools swam downstream over this drop-off, the fish momentarily reoriented themselves and

faced upstream into the current before turning downstream again and continuing their migration. The same behavior was observed in several schools; possibly this sudden reorientation was a result of momentary loss of visual contact with the bottom.

Active vs. Passive Migration

Migrating smolts generally swim downstream actively. Large numbers of smolts seen entering the outlet of Karluk Lake were oriented facing downstream and swimming faster than the current. In Brooks River, Coville Lake outlet, and Naknek River, nearly all smolts observed were facing downstream.

Under certain natural conditions, however, passive displacement downstream has been observed. Foerster (1929) noted continuous passive downstream drift of yearling smolts in the outlet of Cultus Lake. He contrasted this behavior with that of migrating fry that speed singly and rapidly downstream, headfirst. Barnaby (1944) also observed in Karluk River that smolts headed upstream when migrating in areas with appreciable current. On the other hand, Hoar (1953) found in studies in experimental tanks that yearling smolts experiencing a small but sudden elevation in temperature often swam vigorously and rapidly with the current.

Other observations of smolts being passively displaced downstream were attributed to unusual influences such as nets, lights, and falls. In Brooks River, smolts swimming downstream immediately faced upstream upon entering the wings of fyke nets. They maintained their position briefly before the current of 3–4 ft/sec carried them into the net. During darkness when the narrow beam of an underwater hand lamp was directed across Brooks River at right angles to the current, downstream migrating smolts passed quickly through the beam with no change in rheotactic response. When the light was directed obliquely upstream and held on an individual smolt for 1–2 sec, the smolts usually reoriented upstream and passively drifted from view. Smolts observed below Brooks River Falls were tumbled about in the fall pool before they apparently drifted passively downstream. Most smolts observed 30 yards below these falls were oriented downstream. In the shallow area just below Karluk Lake and immediately above a weir used for counting adult sockeye, most smolts were oriented into or across the current and were carried downstream by it. Only 100 yards above this weir in the outlet, smolts were usually actively swimming with the current. It is possible that this aberrant behavior was caused by visual and rheotactic responses of smolts to the weir, which crossed the river. R. Straty (personal communication) noted for several years at the Naknek River adult salmon-counting weir that schools of smolts held above the weir for some time before passing through it. The fish faced upstream as the school moved back and forth across the river immediately above the weir.

There is convincing evidence that smolts also migrate actively through lakes on their way to the outlet rivers. Smolts migrating down the Babine Lake basin complex in spring moved more rapidly than water currents and

averaged 3.2 miles per day in 1960 and 4.9 miles in 1961 (Johnson and Groot, 1963). Burgner (1962) estimated the average rate of travel of a marked smolt at 4–5 miles per day in the Wood River system. These travel rates greatly exceed downlake water currents in either system. Field observations by Groot (1965) at Babine Lake show that within the lake, seaward migration is "...a well-oriented movement on a rather direct route from all parts of the lake to the outlet." Groot also discovered experimentally that sockeye smolts probably have more than one direction-finding system for locating the outlet. In fact, he postulates three systems: (1) sun-compass; (2) polarized light cues; and (3) an unknown noncelestial system called type-X compass orientation.

PREDATION ON MIGRATING FRY AND SMOLTS

The most important freshwater fish predators on juvenile sockeye in southwestern Alaska are Dolly Varden (*Salvelinus malma*), Arctic char (*Salvelinus alpinus*), rainbow trout (*Salmo gairdneri*), and lake trout (*Salvelinus namaycush*).

Various birds also feed intensively on smolts, especially as the fish are leaving the lakes and entering the outlets. The Arctic Tern (*Sterna paradisaea*) and Glaucous-winged Gulls (*Larus glaucescens*) are the most common avian predators mentioned by Thompson et al. (MS, 1964). R. L. Burgner (personal communication) observed the Bonaparte's Gull (*Larus philadelphia*) to be as active a predator as the Arctic Tern at Lake Aleknagik outlet, Agulowak River, and Little Togiak River in the Wood River system. The simultaneous predation on sockeye smolts by fish from beneath and birds from above is readily observed along migration pathways. Often the activity of fish predators will cause the water to boil during migration of smolts around such areas as the outlets of Coville Lake, Grosvenor Lake (R. L. Wallace, personal communication), Naknek Lake (H. W. Jaenicke, personal communication), and Lake Amanka (C. J. DiCostanzo, personal communication).

Extensive predation on sockeye fry has been reported at Chignik Lake, Alaska, by Bower (1929) and Roos (1959, 1960); in lakes in Kamchatka by Semko (1956); and at Hidden Creek by Hartman et al. (1962). Foerster (1938) noted that heavy fish predation on smolts occurs at Cultus Lake. Ricker (1954) considered it likely that predation on downstream-migrating salmon is an example of mortality that Neave (1955) calls depensatory, where predators of a given abundance take a fixed number of prey during the time of contact, independent of the abundance of prey. Thus the smaller annual fry or smolt populations would experience a greater percentage mortality than the larger populations. This phenomenon recently has been considered to play a major role in causing and maintaining the strong cyclic dominance of certain brood-year strains of Fraser River sockeye (Ward and Larkin, 1964).

Mortality of migrating smolts may also be severe in certain rivers. Smolts leaving Kulik, Beverley, and Nerka lakes in the Wood River system must

pass through the 4-mile-long Agulowak River into Lake Aleknagik. Thompson et al. (MS, 1964) found a large concentration of Arctic char in Lake Aleknagik around the outlet of the Agulowak River during the spring smolt migration period of 1954. They estimated the population size of the char by tag-and-recapture techniques; determined stomach contents and considered digestion rates; and estimated that about 1,300,000 smolts were eaten by the char assembled there. Translated into terms of returning adults, and assuming a conservative average of 15% marine survival, this represents a loss of 195,000 adults returning to the fishery and spawning grounds.

Arctic char are abundant in and around other lake-connecting rivers in the Wood River system. Aspinwall (1963) observed them in Little Togiak River feeding heavily during the night on smolts. One char captured contained 16 sockeye smolts in its stomach.

When sockeye smolts leave Karluk Lake, sizable schools of Dolly Varden congregate in the lake outlet. Heavy predation by these char on the smolts has been observed night after night.

Lake trout also prey on smolts migrating through some rivers that connect lakes. Lake trout actively feed on sockeye smolts in the Narrows between Nuyakuk and Tikchik Lakes in the Wood River system (R. L. Burgner, personal communication). At Coville Lake, on May 27, 1963, the stomachs of seven of nine lake trout caught at the outlet contained smolts. The number of smolts per stomach ranged from 23 to 41 (average, 32).

Another factor that affects different smolt populations disproportionately is the length and nature of the travel route through single-lake or multilake systems. Smolts leaving Coville Lake in the Naknek River system pass through its outlet, then the outlet of Grosvenor Lake, and finally the trunk river outlet from Naknek lake (Fig. 1). They are vulnerable to predation in all three outlets. In the Wood River system, smolts from Lake Kulik have to negotiate four lake outlets to reach salt water, whereas smolts from the lowest lake in the system, Lake Aleknagik, have to pass through only one (Fig. 1). Predation on smolts occurs in each of the four outlets in the Wood River system according to R. L. Burgner (personal communication). If predation on smolts is an important limiting factor in determining size of adult populations, are there mechanisms in the biotic potential of lower and upper lake populations such as differences in fish size, fecundity, or age at maturity, that compensate for the differences in the total length of streams that migrating smolts must pass through? Data are not yet available to evaluate these factors, although Ricker (1966) discusses the possibility of a depensatory relation between smolts of different stocks migrating through a common trunk stream.

MIGRATORY HABITS AND SURVIVAL

Time of Migration and Survival

Most fry and smolts migrate when environmental opportunities in the lakes and oceans are most favorable for their survival and growth. Early spring migrations of fry coincide with the start of the growing season in the

lakes, when water temperatures rise, plankton blooms, and the rate of growth of fish increases (fry become less vulnerable to predation as they increase in size). Foerster (1938) reported that mortality of young-of-the-year sockeye at Cultus Lake declined rapidly as the first growing season progressed. The early spring migrations of most smolt populations to salt water also coincide with the start of the growing season. A further possible advantage of migration in early spring is that food needs of piscivorous predators may be minimal because of the cold water temperatures.

Exceptions to this apparently propitious seasonal timing of migration occur. Spawning occurs in both summer and fall in Meadow and Canyon creeks at Karluk Lake. Fry from summer spawners emerge and migrate into Karluk Lake in April; fry from fall spawners emerge and migrate in late June and early July. These late-migrating fry miss the first part of the growing season. They are undoubtedly smaller throughout the summer than early spring migrants and may well be at a survival disadvantage in the face of predation, especially over the long winter period. Compensatory mechanisms are likely to be operating in this instance. If fall spawners are more fecund than spring spawners, this could well be an adaptive response by the fall spawning population to a higher mortality, as Nikolsky (1963, p. 152–153) might suggest.

Behavior and Survival

Predation has been shown to be a serious cause of freshwater mortality of migrating sockeye fry and smolts at certain times, especially when the smolts leave the lakes and are confined to rivers along the migration route. The migratory behavior of these juvenile sockeye seems to be adapted to minimize the mortality from predators.

We do not want to overemphasize predation as a major mortality factor on sockeye survival. Tremendous losses in freshwater are related to many other biological, physical, and chemical factors. Yet, in the migratory phase of life history for fry and smolts, predation must be extremely critical to survival.

The usual schooling of smolts would seem to promote survival in at least two ways. The incidence of contact between predator and prey is probably reduced, especially during open-lake migration, because prey are grouped at specific points rather than distributed generally. Probably the function of the school after predators have made contact is of greater importance. The school may present a more formidable aspect to predators than randomly distributed individuals. Unfortunately, few observations have been recorded on the behavior of prey under attack by predators. Whether schooling of certain prey species is advantageous in reducing losses to predators in certain situations is still mostly conjecture.

The theoretical problem involved in sending unescorted ships across the ocean, subject to discovery by enemy submarines, is similar to this problem. The basic theory was published by Koopman (1956) and adapted to fish

schooling and predation by Brock and Riffenburgh (1959). Olson (1964) presented a simple example illustrating that the probability of a small fish being eaten when swimming alone was substantially higher than if it were in a school.

Rapid travel through outlet streams during the darkest hours also must enhance greatly the chances of survival of both fry and smolts. Downstream migrations of smolts are mainly confined to the darkest hours of the night, when the chances of visual perception by predators may be at a minimum. The downstream orientation during migration of fry in certain streams and of smolts in most, if not all, rivers should aid more effectively than passive downstream displacement would in the detection of potential predators and allow greater opportunity for escape; swimming with the current also helps to minimize the period of exposure to predation.

PATTERNS OF JUVENILE MIGRATORY BEHAVIOR

Sufficient data are now available to outline the broad scheme of behavior with regard to phototaxis, rheotaxis, and schooling of sockeye from fry to smolts. The general pattern during the spring emergence of sockeye fry from the gravel in tributaries leading into lakes is one of negative phototaxis, restricting migration almost completely to the darkest hours of the night. Fry migrate individually, are negatively rheotactic, face downstream during migration, and swim actively. Fry emerging directly into the lakes from lake beach spawning areas presumably quickly adopt the behavior of lake residents described below.

Shortly after fry enter the nursery lake or after extensive holding en route, schooling takes place; and it continues to some extent at least during the remainder of their residence in the nursery lakes. A sharp change from negative phototaxis accompanies or is an immediate prerequisite to schooling — a behavior which is strongly related to visual stimuli and feeding (Hoar, 1956; McDonald, 1960). Their phototactic behavior during this period is neither strictly negative nor positive. Some young-of-the-year at Karluk Lake are normally present in very shallow littoral areas during daylight in June and July. Some young sockeye remain in Brooks River well into late summer and actively school and feed during the daylight. Young sockeye in open-lake waters however are to some extent negatively phototactic. They are found at or near the surface at night and usually much deeper during daylight (Johnson, 1958; Pella, 1964). Pella presents Lake Aleknagik survey echograms taken periodically over 24-hr periods. The ascent of young sockeye to the surface at dusk and their descent to deeper depths at dawn are dramatically evident in the echograms.

The limited observations reported suggest that they are now positively rheotactic, a behavior mechanism that could be a major factor in confining juvenile sockeye to the lakes during the rearing period (Hartman et al., 1962). This conclusion was strengthened by observations on three releases of fry in the current at the outlet of Brooks Lake in 1964. Each school of 30–50 fry

was followed underwater by divers, and was seen to move directly and constantly upcurrent into the lake proper. Attempts to block and panic the fry only momentarily disrupted their upstream movements, which were resumed when the diver moved away to the limit of visual contact by the diver with the fry.

Sockeye smolts are schooled as they migrate to the sea. Groot (1965) found them well oriented, schooled, and actively migrating, most especially at night in Babine Lake. In the rivers, they continue the greatest activity at night, are generally negatively rheotactic, and actively swim downstream with the current. The fry and smolts migrating downstream differ only in their schooling behavior: fry are usually unschooled, smolts are usually schooled. In some British Columbia rivers, smolts under total darkness apparently become unschooled and migrate as individuals until daylight when schooling again occurs (Howard Smith, personal communication). In Bristol Bay, however, total light extinction seldom occurs during nocturnal migrations in late May and early June, as evidenced by photometer readings at Brooks Lake. Schooling of smolts seems more persistent there throughout nocturnal migrations.

Several complicated exceptions to this general scheme, especially for fry migrations, indicate the spectrum of behavioral response to different environmental conditions. Normally, after short downstream migrations from natal tributaries, sockeye fry school when they first reach the lakes. In some instances where downstream migration requires 2 or 3 days of travel, sockeye fry tend to school during daylight holding periods (McDonald, 1960) and probably remain schooled thereafter. Rheotactic response sometimes shifts briefly from negative to positive among both migrating fry and smolts, and migration continues by passive displacement downstream. This shift may be associated with loss of relevant visual contact with river bottoms as suggested by Stuart (1962), especially in deep rivers or large pools. Upstream migrations of fry from spawning areas in lake outlets such as at Lake Chilko (Andrew and Geen, 1960) and Karluk Lake occur several days, if not weeks, after emergence. These fry, at Karluk at least, are usually schooled and migrate during daylight along the river banks (Robert F. Raleigh, personal communication). There are, however, even more complicated situations than these. Andrew and Geen (1960) report the "Sockeye fry produced by spawning in the South Thompson River below Little Shuswap Lake (Fraser River system) pass upstream through this lake and, after swimming upstream through Little River, enter Shuswap Lake (their usual rearing area)." And finally an extremely complicated fry behavior is reported by Ricker (1966). He notes that at Morris Creek in British Columbia, emerged sockeye fry "... first go downstream, then swim through a few hundred meters of practically slack water, then turn upstream into the Harrison River at the head of the rapids and proceed into Harrison Lake."

While this paper was in final editorial review, P. McCart published his fine paper on the behavior and ecology of sockeye salmon fry in the Babine

River (McCart, 1967). His observations on downstream and upstream fry migration behavior strongly support our main conclusions, and he has added considerable detail to our knowledge of upstream fry migrations.

ACKNOWLEDGMENTS

Mr Herbert W. Jaenicke of the Auke Bay Biological Laboratory has been field supervisor of research on sockeye smolts at Naknek, Becharof, and Ugashik lakes since 1959. We wish to acknowledge his generous contribution of unpublished data, his detailed analyses of some of the data for us, and his review of the manuscript. We also acknowledge for review of the manuscript Dr Charles J. DiCostanzo of the Auke Bay Biological Laboratory; Dr Robert L. Burgner, Dr Ole Mathisen, and Mr Orra E. Kerns, Jr., of the University of Washington; and Dr R. E. Foerster of the Fisheries Research Board of Canada, Biological Station, Nanaimo, British Columbia.

REFERENCES

ANDREW, F. J., AND G. H. GEEN. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. Intern. Pacific Salmon Fish. Comm., Bull. XI. 259 p.

ANON. MS, 1964. Skeena Salmon Management Committee Annual Report for 1963. Fish. Res. Bd. Canada, Biol. Sta., Nanaimo. 47 p.

ASPINWALL, N. 1963. Little Togiak River smolt enumeration, 1961. Fish. Res. Inst., Univ. Wash., Circ. No. 181. 14 p.

BAGGERMAN, BERTHA. 1960. Factors in the disdromous migrations of fish. Symp. Zool. Soc. London, **1**: 33–60.

BARNABY, JOSEPH T. 1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum), of the Karluk River, Alaska. U.S. Fish Wildlife Serv., Fish Bull., **50**(39): 237–295.

BOWER, WARD T. 1929. Alaska fishery and fur-seal industries in 1927. U.S. Bur. Fish. Rept. Comm. Fish. for 1928 with appendixes. Pt. 1. p. 61–171. (Doc. No. 1040, issued February 1, 1929.)

BRETT, J. R., AND D. F. ALDERDICE. 1959. Research on guiding young salmon at two British Columbia field stations. Bull. Fish. Res. Bd. Canada, No. 117. 15 p.

BRETT, J. R., AND J. A. MCCONNELL. 1950. Lakelse Lake sockeye survival. J. Fish. Res. Bd. Canada, **8**(2): 103–110.

BROCK, VERNON E., AND ROBERT H. RIFFENBURGH. 1959. Fish schooling: a possible factor in reducing predation. J. Conseil Conseil Perm. Intern. Exploration Mer, **25**(3): 307–317.

BURGNER, R. L. 1962. Studies of red salmon smolts from the Wood River Lakes, Alaska. Univ. Wash. Publ. Fish. (N.Y.), **1**: 247–314.

CHAMBERLAIN, F. M. 1907. Some observations on salmon and trout in Alaska. U.S. Bur. Fish. Rept. Comm. Fish. for 1906 and Spec. Papers. 112 p. (Doc. No. 627, issued December 18, 1907.)

FOERSTER, R. E. 1929. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia, No. 1. Introduction and the run of 1925. Contrib. Canadian Biol. Fish., (N.S.), **5**(1): 1–35.

1937. The relation of temperature to the seaward migration of young sockeye salmon (*Oncorhynchus nerka*). J. Biol. Bd. Canada, **3**(5): 421–438.

1938. An investigation of the relative efficiencies of natural and artificial propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. J. Fish. Res. Bd. Canada, **4**(3): 151–161.

1952. The seaward-migrating sockeye and coho salmon from Lakelse Lake, 1952. Fish. Res. Bd. Canada, Pacific Prog. Rept. No. 93. p. 30–32.

FORESTER, R. E., AND W. E. RICKER. 1953. The coho salmon at Cultus Lake and Sweltzer Creek. J. Fish. Res. Bd. Canada, **10**(6): 293–319.

GROOT, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour, Suppl. 14. 198 p.

HARTMAN, WILBUR L., WILLIAM R. HEARD, AND CHARLES W. STRICKLAND. MS, 1961. Red salmon studies, Field Operations Report, 1960, Brooks Lake Laboratory. Bur. Comm. Fish., Biol. Lab., Auke Bay, Alaska. 54 p.

HARTMAN, WILBUR L., CHARLES W. STRICKLAND, AND DAVID T. HOOPES. 1962. Survival and behavior of sockeye salmon fry migrating into Brooks Lake, Alaska. Trans. Am. Fish. Soc., **91**(2): 133–139.

HARVEY, H. H. 1963. Pressure in the early life history of sockeye salmon. Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 257 p.

HEARD, WILLIAM R. 1964. Phototactic behaviour of emerging sockeye salmon fry. Animal Behaviour, **12**(2): 382–388.

HOAR, WILLIAMS S. 1953. Control and timing of fish migration. Biol. Rev., **28**(4): 437–452.
1954. The behaviour of juvenile Pacific salmon with particular reference to the sockeye (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada, **11**(1): 69–97.
1956. The behaviour of migrating pink and chum salmon fry. Ibid., **13**(3): 309–325.

JAENICKE, HERBERT W. MS, 1963. Ugashik River smolt studies, a preliminary report of the season. Bur. Comm. Fish., Biol. Lab., Auke Bay, Alaska. 32 p.

JOHNSON, W. E. 1958. Density and distribution of young sockeye salmon (*Oncorhynchus nerka*) throughout a multibasin lake system. J. Fish. Res. Bd. Canada, **15**(5): 961–982.

JOHNSON, W. E., AND C. GROOT. 1963. Observations on the migrations of young sockeye salmon (*Oncorhynchus nerka*) through a large, complex lake system. Ibid., **20**(4): 919–938.

KERNS, ORRA E., SR. 1961. Abundance and age of Kvichak River red salmon smolts. U.S. Fish Wildlife Serv., Fish. Bull., **61**(189): 301–320.

KOOPMAN, B. D. 1956. The theory of search. II. Target detection. Operations Res., **4**: 503–531.

KROGIUS, F. V., AND E. M. KROKHIN. 1948. [On the production of young sockeye salmon (*Oncorhynchus nerka* Walb.).] Izv. Tikhookeans. Nauchn. Issled. Inst. Rybn. Khoz. i Okeanog., **27**: 3–27. (Fish. Res. Bd. Canada, Transl. Ser. No. 109.)

MCCART, P. 1967. Behavior and ecology of sockeye salmon fry in the Babine River. J. Fish. Res. Bd. Canada, **24**(2): 375–428.

MCDONALD, J. 1960. The behaviour of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. J. Fish. Res. Bd. Canada, **17**(5): 655–676.

MEEHAN, W. R. 1966. Growth and survival of sockeye salmon introduced into Ruth Lake after removal of resident fish populations. U.S. Fish Wildlife Serv., Spec. Sci. Rept. Fish., **532**: 18 p.

NARVER, DAVID WELLS. MS, 1963. Identification of adult red salmon groups by lacustrine scale measurement, time of entry, and spawning characteristics. M.Sc. Thesis. Univ. Wash., Seattle, Wash. 96 p.

NEAVE, FERRIS. 1955. Notes on the seaward migration of pink and chum salmon fry. J. Fish. Res. Bd. Canada, **12**(3): 369–374.

NIKOLSKY, G. V. 1963. The ecology of fishes. Academic Press, Inc., New York. 352 p. (Translated from Russian by L. Birkett.)

OLSON, F. C. W. 1964. The survival value of fish schooling. J. Conseil Conseil Perm. Intern. Exploration Mer, **29**(1): 115–116.

PARKER, ROBERT R., AND ROBERT E. VINCENT. 1966. Progress report in research studies at the Kitoi Bay Research Station. Alaska Dept. Fish. Ann. Rept. 1955. p. 25–27.

PELLA, J. J. 1964. Sockeye salmon fry distribution and growth in Lake Aleknagik, Alaska, during the summer of 1962. M.Sc. Thesis. Univ. Wash., Seattle, Wash. 132 p.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd. Canada, **11**(5): 559–623.
1966. Sockeye salmon in British Columbia. *In* Salmon of the North Pacific Ocean, Pt. 3. Intern. North Pacific Fish. Comm. Bull. No. 18. p. 59–70.

ROOS, J. F. MS, 1958. Red salmon smolt studies at Chignik in 1958. Fish. Res. Inst., Univ. Wash. 17 p.
1959. Feeding habits of the Dolly Varden, *Salvelinus malma* (Walbaum), at Chignik, Alaska. Trans. Am. Fish. Soc., **88**(4): 253–260.
1960. Predation of young coho salmon on sockeye salmon fry at Chignik, Alaska. Ibid., **89**(4): 377–379.

SEMKO, R. S. 1954. [The stocks of west Kamchatka salmon and their commercial utilization.] Izv. Tikhookeans. Nauchn. Issled. Inst. Rybn. Khoz. i Okeanog., **41**: 3–109. (Fish. Res. Bd. Canada, Transl. Ser. No. 288.)
1956. [The influence of predation on numbers of young salmon.] Tr. Probl. Temat. Soveshch., Akad. Nauk. SSSR Zool. Inst. Moscow, **6**: 148–149.

STUART, T. A. 1962. The leaping behaviour of salmon and trout at falls and obstructions. Dept. Agr. Fish. Scotland, Freshwater and Salmon Fish. Res., **28**: 1–46.

THOMPSON, RICHARD B., CHARLES R. WEAVER, AND WILLIAM D. GRONLUND. MS, 1964. A study of the role of the Arctic char, *Salvelinus alpinus*, as a salmon predator in the Wood River Lakes, Alaska, with notes on its life history. Bur. Comm. Fish., Biol. Lab., Seattle, Wash. 60 p.

THOMPSON, SETON H. MS, 1964. The red salmon (*Oncorhynchus nerka*) of Copper River, Alaska. Bur. Comm. Fish., Biol. Lab., Auke Bay, Alaska. 139 p.

THORSTEINSON, FREDRIK V., AND JOHN ROOS. MS, 1958. A report of studies on red salmon smolts carried out at Chignik in 1955 and 1956. Fish. Res. Inst., Univ. Wash. 22 p. + appendix.

WARD, F. J., AND P. A. LARKIN. 1964. Cyclic dominance in Adams River sockeye salmon. Intern. Pacific Salmon Fish. Comm., Prog. Rept. No. 11. 116 p.

Unusual Fishes Taken by Midwater Trawl off the Queen Charlotte Islands, British Columbia[1]

By F. H. C. Taylor

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

On three cruises in 1964 and 1965 the CGS *G. B. Reed* midwater-trawled beyond the continental slope south and west of the Queen Charlotte Islands to determine the types of fish associated with the open ocean sound-scattering layers. The fish taken included seven species not previously reported from British Columbia, and four which are second records. Species not previously reported from British Columbia are: *Sagamichthys abei*, *Notolepis rissoi rissoi*, *Scopelosaurus harryi*, *Borodulina infans*, *Serrivomer jesperseni*, *Oneirodes acanthias*, and *Chaenophryne*, cf. *parviconus*. Species reported once before include: *Bathylagus ochotensis*, *Nansenia candida*, *Caristius macropus*, and *Oneirodes eschrichti*-group.

INTRODUCTION

In 1964 and 1965, the Fisheries Research Board of Canada trawler, CGS *G. B. Reed*, surveyed the general area south and west of the Queen Charlotte Islands (Fig. 1) to determine the types of fish associated with ocean sound-scattering layers. Three midwater trawl cruises were made, June 6–23, 1964, October 27 to November 14, 1964, and July 8–18, 1965.

Details of the equipment used and of the location, time, and depth of each haul, the number of each species caught (Taylor, 1967a) and observations on the sound-scattering layers, and on the relation to them of the major species of fish taken (Taylor, 1967b) are described elsewhere. This report is limited to descriptions of the more unusual bathypelagic fish taken and records several species not previously reported off British Columbia or known from only one or two specimens. It extends Peden's (1966) summary of species not previously known from British Columbia that have been reported since the publication of Clemens and Wilby's (1961) monograph. The detailed descriptions follow the general pattern used by Clemens and Wilby. The species described had suffered appreciable net damage and in most cases were beyond the point where photographs were worthwhile.

The collections made on the first and second cruises are in the National Museum of Canada; a part of the collection of the third cruise is there also and a part at the Institute of Fisheries, University of British Columbia. The fish have been identified by Dr D. E. McAllister of the National Museum of Canada, Mrs Isabel Radforth of the Royal Ontario Museum (Myctophidae from part of the third cruise), and by the staff of the Institute of Fisheries of the University of British Columbia.

[1]Received for publication May 19, 1967.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

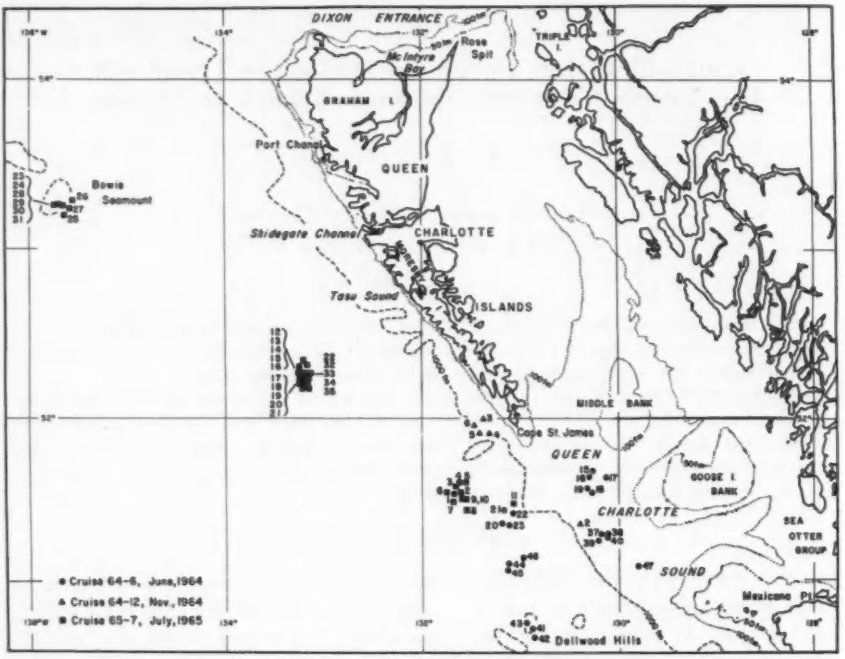

FIG. 1. Map of the northern and central British Columbia coast showing the location of hauls made beyond the continental shelf.

SEARSIDAE

SAGAMICHTHYS ABEI? PARR, 1953

A single specimen, 89.5 mm in standard length, most probably of this species, was caught on July 11, 1965, at 52°11′N, 133°11W′ (52 nautical miles[2] southwest of Tasu Sound, Queen Charlotte Islands) from 510 to 595 m over a bottom depth of 2650 m. This specimen is in collection No. NMC65-300, National Museum of Canada. A second specimen (NMC65-298) of this family was caught nearby at 52°18′N, 133°13′W in 185 to 275 m over bottom depths of 2600 to 2750 m. It was 37.3 mm in standard length but badly damaged. It has tentatively been referred to this species. These specimens represent the first records of the species off British Columbia.

In the 89.5-mm specimen, the body is elongate, deepening anteriorly to the nape. Head large, compressed; snout pointed; mouth terminal, large, maxillary extending to a point behind eye; teeth small, pointed, on jaws, vomer, and palatines. Gill rakers slender, 24, branchiostegals 9, pyloric caeca 25. Fins: dorsal (1), 19; anal, 16; pelvics abdominal, 10; pectorals, 17; caudal furcate. Lateral line, almost straight. Scales cycloid, small, in transverse rows

[2]A nautical mile is equivalent to 1.85 km.

about 104, in lateral line enlarged about 45, scales of head with reverse imbrication. Photophores: GO (gular organ, between mandibles), dumbell shaped; BR (branchiostegal) 7; JO (jugular organ), THO (thoracic organ), and PVO (preventral organ), on midventral line, barlike; SVO (supraventral organ), SAO (supra-anal organ), PAO (postanal organ), ICO (infracaudal organ), and supraorbital body all present. A shoulder organ is present, discharging through a black tube just below lateral line above pectoral fin. This specimen fits the description of *S. abei* except for the following differences: 9 branchiostegal rays instead of 6, the GO is dumbell shaped instead of circular, and the pectoral fin has 17 rays instead of 14. The 37.3-mm specimen had no photophores developed except for a gular organ and a supraorbital body.

Length to 9 inches (22.9 cm).

Range: Lavenberg and Grinols (MS, 1965) have identified *S. abei* from the Antarctic, off Japan, California, Oregon, Washington, and questionably from off British Columbia.

ARGENTINIDAE

Bathylagus ochotensis Schmidt, 1938

Nineteen specimens of this argentinid were taken off the Queen Charlotte Islands, 16 miles west, 30–35 nautical miles south-southwest and 53 nautical miles southeast of Cape St. James. The collections were made in 1964 on June 15 and 20, and October 28 and 29, and in 1965 on July 9. The depth of capture varied from near the surface to 730–825 m, the water depth from 860 to 2380 m. The specimens are in the National Museum of Canada collection No. NMC65-296, NMC66-26, -31, -36, -39, and -40.

This species was first reported off British Columbia by McAllister (1959) who describes a specimen taken about 340 miles west of Kyoquot Sound (50°N, 135°W). Aron (1960) collected 967 specimens between southern California and the Aleutian Islands; of these 53 could be considered as taken off British Columbia (north of 48°30′N) but well offshore, and 2 near the Aleutian Islands (50°47′N, 174°31′W).

In the description below, the counts in parentheses are from non-British Columbia material (Cohen, MS, 1957).

Body elongate, slender; caudal peduncle stout. Head moderate, compressed; snout short, somewhat pointed; mouth terminal, small; maxillary not reaching eye; branchiostegals 2; teeth small, on dentaries, palatines, and vomer, none on tongue; eye moderate, 2.9 to 3.0 in head; interorbital space nearly flat; median occipital ridge slight; operculum with downwards directed striae. Gill rakers 7 + 16 to 17 (14,15) = 23 to 24. Fins: dorsal (1) 10 to 11 (12); adipose small; anal 14 to 15 (16); pelvics abdominal, 10(11); pectoral 10 (11); caudal furcate. Lateral line, present. Scales: cycloid, moderate, deciduous, in oblique rows about 45 to 47. Colours: blackish on body; mouth, gill cavity, and peritoneum black.

Length to 4.75 inches (12.1 cm).

Range: In the eastern Pacific, from southern California to the Aleutian Islands, also known from Japan and the Okhotsk Sea.

NANSENIA CANDIDA COHEN, 1958

A total of 22 specimens of this argentinid were present in five hauls from three localities — 50 nautical miles southwest of Tasu Sound (about 52°17′N, 133°10′W), 30–35 nautical miles south-southwest of Cape St. James (about 51°26′N, 131°09′W), and 53 nautical miles southeast of Cape St. James (about 51°16′N, 130°07′W). Two were collected in 1964 on June 15 and 20, the remainder in 1965 between July 8 and 12. They were taken at depths of 730–825 m in the daytime, and at 100–330 m in the early evening. The water depth was between 2200 and 2750 m. In addition to the 22 identified specimens, 36 more were recorded as *Nansenia* sp. were taken in 1965 in the same general localities.

This species, described by Cohen (1958) from five specimens from California, was first recorded off British Columbia by McAllister (1959) from a specimen taken in a 6-ft Isaacs-Kidd trawl 340 miles west of Union Island, Kyoquot Sound (50°N, 135°W). Aron (1960) reported one specimen taken at 45°46′N, 146°25′W. Of specimens listed as *Nansenia* sp. he reports none north of 50°N, 55 between 50°N and 48°N, and 30 south of 48°N.

In the description below, counts in parentheses are from extralimital material (Cohen, 1958):

Body elongate, slender; caudal peduncle, stout. Head moderate, compressed; snout somewhat pointed; mouth terminal, small, maxillary not or just reaching eye; branchiostegals 3; teeth, small; eye, moderately large, diameter 2.7 to 3.0 in length of head; interorbital space slightly concave; operculum smooth; median occipital ridge absent. Fins: dorsal (1) 10–11 (10-12); adipose, small; anal 9–11 (10–11); pelvic abdominal 10–11 (10); pectoral 10–11 (11–12); caudal furcate. Gill rakers 28–31 (30). Pyloric caeca 8–10 (9). Lateral line, inconspicuous. Scales: cycloid, moderate, deciduous, in lateral line about 43–46 (45 and 47). Colour: dark brown on body and head, lighter below, bluish tissue on nape, preopercular and gular regions.

Length to 6.5 inches (16.5 cm).

Range: California to northern British Columbia.

The specimens are in the National Museum of Canada collections No. NMC65-291, -292, -299B, -300, -303, NMC66-26, and those identified as *Nansenia* sp. in the Institute of Fisheries collections No. BC65-607, -609, -610, -615, -623, and -624.

PARALEPIDAE

NOTOLEPIS RISSOI RISSOI (BONAPARTE, 1938)

Four specimens were taken in the general area 30–50 nautical miles southwest of Cape St. James, Queen Charlotte Islands; two on June 15, 1964, from 730–825 m at 51°26′N, 131°09′W, one on June 22, 1964, from 230–255 m at 51°07′N, 131°04′W, and one on July 9, 1965, from 155–185 m at 51°30′N, 131°34′W. These catches represent the first definite records of this species from British Columbia waters and extends its range in the eastern

Pacific northward some 200 nautical miles. This species was originally described from the United States side of the Strait of Juan de Fuca. Additional specimens have been caught in Pugat Sound (2), off southern California (6), and off Japan (1) (Grinols, MS, 1965). The midwater trawl specimens are in the National Museum of Canada collections No. NMC66-26, -33 and NMC65-295.

Body elongate, slender, compressed, depth at nape about 11–12 in standard length; fleshy carinae between anus and anal fin moderately developed. Head elongate, compressed, length 3.8–4.3 in standard length; snout elongate, pointed; interorbital space concave with two longitudinal ridges; mouth terminal, moderate, not reaching vertical from eye, tip of lower jaw slightly elevated. Teeth on premaxillaries, 6 small depressible canines followed by a series of small fixed retrose teeth; on mandible numerous small depressible canines in two uneven rows; on palatines, 5 or 6 widely spaced canines followed by a number of small fixed teeth; on tongue a row of small fixed teeth along outer edge. Gill rakers in form of plates, each bearing several small needlelike teeth. Eye small, diameter 6.0–6.8 in head. Fins: dorsal (1) well back on body but with origin in front of pelvic origin; adispose, small; anal, far back on body, large, moderately high; pelvics abdominal; pectorals small; caudal small and furcate. Anus between pelvic fins. Lateral line almost straight, incomplete, ending over middle of anal fin. Scales: in adult only.

Length to 9.25 inches (23.5 cm).

Range: southern California to northern British Columbia, and off Japan.

Harry (1951, 1953) considered that *Paralepis coruscans* Jordan and Gilbert belonged to the genus *Notolepis*; he erected a new subgenus, *Profundisudis* for *N. rissoi* and *N. coruscans*. Rofen (1966) states that with evidence from extensive studies of *N. r. rissoi* and *N. r. krøyeri* at hand there is reason to believe *P. coruscans* is a synonym for *N. r. rissoi*. He notes one slight difference between *coruscans* and *r. rissoi* whereby in dorsal-to-ventral fin distance *coruscans* is closer to *r. krøyeri* than to *r. rissoi*. This difference he attributes to a difference in size of the specimens. Such a difference does not occur in the present specimens, which agree well in counts and measurements with *r. rissoi*.

Counts and body proportions of two of the specimens taken are as follows.

	Standard length	218 mm	200 mm
Counts:	Dorsal fin rays	9	10
	Anal fin rays	29	32
	Pectoral fin rays	11	11
	Pelvic fin rays	9	9
	Lateral line pores	61	61
Body proportions:	(thousands of standard length)		
	Head length	243	243
	Snout length	119	118
	Maxillary length	92	98
	Diameter of orbit	36	40

(*Continued*)

	Standard length	218 mm	200 mm
Body proportions:	Width of bony interorbital	28	29
	Postorbital length	85	88
	Anterior margin of orbit to nostril	25	28
	Body depth (nape)	89	83
	Body depth (dorsal origin)	85	65
	Least depth, caudal peduncle	21	21
	Length, caudal peduncle	37	35
	Snout to origin of dorsal	652	660
	Snout to origin of anal	812	802
	Snout to origin of adipose	952	954
	Snout to origin of pectoral	243	255
	Snout to origin of pelvics	702	691
	Dorsal origin to anal origin	193	168
	Dorsal origin to pectoral origin	404	420
	Dorsal origin to pelvic origin	99	68
	Pectoral origin to pelvic origin	449	435
	Length of dorsal base	32	31
	Length of anal base	156	157

SCOPELOSAURIDAE

Scopelosaurus harryi (Mead, 1953)

Two specimens were taken, representing the first British Columbia records, one on June 15, 1964, at 51°26′N, 131°09′W (30 nautical miles southwest of Cape St. James) at a depth of 730–825 m, the other on July 11, 1965, at 52°11′N, 133°11′W (52 nautical miles southwest of Tasu Sound) at a depth of 510–595 m. This species was previously known only from the type specimen (38.4 mm in standard length) taken off Iwate Prefecture, Japan (Mead and Taylor, 1953). The recorded range is thus extended east across the Pacific. The specimens are in the National Museum of Canada, collection No. NMC65-300 and NMC66-26. In the description below the body proportions and fin ray counts of the holotype are shown in parentheses.

Body elongate, slender, cylindrical, body depth 9.7–11.1 (13.7) in standard length. Head elongate, somewhat wedge shaped, 4.0–4.1 (4.3) in standard length; snout long, pointed, rather spatulate, 2.9–3.1 (3.1) in head length; interorbital space wide, with 3 slight ridges; lower jaw projecting slightly; premaxillary extending back to last one-fifth of orbit; orbit 5.2 (3.5) in head length; eye with lens located in posterior part of pupil; teeth small, sharp on jaws, palatines and vomer; tongue toothless. Gill rakers slender 1 + 18 or 19 = 19 or 20 (2 + 18 = 20). Anus, close behind origin of pelvics base; adispose small; anal 16–18 (17); pelvics 9 (10), pectoral 10–11 (10); caudal straight. Two rows of pores on jaws. No photophores. Scales: relatively large, cycloid, deciduous on head and body; on lateral line 63, with 3 rows above and below lateral line. Colour, dark on head, body and fins, peritoneum, gills and mouth cavities black.

Length to 8.5 inches (21.6 cm)

Range: off Japan and off northern British Columbia.

Marshall (1966) states that when a greater series of specimens have been examined *Scopelosaurus lepidus* (Krefft and Maul, 1955) may prove to be synonymous with *S. harryi* (Mead). *Scopelosaurus lepidus* is found in the North Atlantic with a few specimens from the South Atlantic, Indian, and Pacific oceans.

NEMICHTHYIDAE

Borodulina infans (?) (Günther, 1878)

Four specimens were collected, one about 30 nautical miles southwest of Cape St. James at 51°29.5′N, 131°03′W in 275–310 m on July 9, 1965, and the others 2 days later, 50 nautical miles southwest of Tasu Sound at 52°11′N, 133°11′W in 510–595 m. These are the first records of this species in British Columbia and extend its range north from the Gulf of Panama.

The specimens had all suffered some degree of damage, so that measurements and counts could be made on only one, and either counts or measurements on one other. The specimens are in the collection of the Institute of Fisheries, University of British Columbia.

Body very elongate, extremely slender, tapering posteriorly to a sharp point, greatest depth of body about 46 in total length. Head elongate, length about 10 in total length; mouth terminal, deeply cleft, jaws prolonged, slender, recurved with toothed pad on tips; lower jaw shorter about 1.4 in upper jaw; jaws with rows of simple pointed teeth. Eye small, about 15–16 in head length, barely entering dorsal profile of head. Anus remote from head, the distance from snout to anus comprising about one-eighth the total length (Fig. 2, *lower*). Fins: dorsal (1) about 300–350 rays (one specimen about 345–350, another about 301), extending from just behind pectoral; anal about 265–270 rays — this count may be low because of damage to the ventral surface near the anus. Roule and Bertin (1929) give the anal fin ray count as 20–30 less than the dorsal. The origin of the anal fin is immediately behind the anus. Pelvics absent; pectorals small; caudal very small, short. Lateral line slightly decurved, then straight; pores in a single row about 188 and 191 in 2 specimens, large and open. Scales absent. Colour, dusky brown, somewhat lighter on belly.

Length to 18 inches (45.7 cm).

Range: Atlantic, Indian, and Pacific oceans.

Roule and Bertin (1929) consider *Nemichthys infans* Günther, 1878, *Labichthys elongatus* Gill and Ryden 1883, *Labichthys gilli* Bean 1891, and *Labichthys bowserii* Garman 1899 conspecific and for reason of priority should be called *Avocettina infans* (Günther) 1878. Whitely (1931) states that *Avocettina* 1888 Jordan and Davis (Pisces) is preoccupied by *Avocettina* Mulsont and Verreaux 1866 (Aves). He provides a substitute name *Borodinula* Whitley, 1931. Thus this species should be called *Borodinula infans* (Günther) 1878. Roule and Bertin (1929) find body proportions generally unreliable for specific differentiation in this genus. The number of dorsal rays is given as 300–350, of anal rays as 20–30 less, and of lateral line pores as 178–191.

Chapman (1940) considers *gilli* (Bean) 1891, recorded from northern British Columbia and Alaska, to be a distinct species on the basis of the lower number of dorsal rays (260), of anal rays (205), and of lateral line pores (156). The counts for these characters on the four trawled specimens exceed those for *gilli* and fall within the range of *infans*. In addition these specimens agree with the latter in such less specifically decisive ways as ratio of trunk depth to trunk length, of diameter of orbit to postorbital distance, and of postorbital distance to ano-pectoral distance. They have therefore been referred to *Borodinula infans*.

SERRIVOMERIDAE

Serrivomer jesperseni Bauchot-Boutin, 1953

This species was taken for the first time off British Columbia on June 15, 1964, at 51°36′N, 131°09′W (30 nautical miles south by west of Cape St. James) at 730–825 m in water 2290–2380 m deep. The recorded range is thus extended northward some 2650 nautical miles from the Gulf of Panama. The single specimen, about 424 mm in total length is in the National Museum of Canada, collection No. NMC66-26.

In the description below the counts in parentheses are from Bauchot (1959).

Body very elongate, extremely slender, tapering posteriorly to a sharp point; greatest body depth about 42 in total length. Head elongate, about 5.3 in total length; mouth terminal, deeply cleft; jaws prolonged, slender without toothed pad at tip, little recurved, lower jaw longer than upper; jaws with rows of teeth of *longidentatus* type, inner row enlarged; vomer with 49 large bladelike teeth forming a semicircular plate (Fig. 2, *upper*). Eye small, about 19 times in head. Anus remote from head, distance from snout to anus about one-quarter of total length. Fins: dorsal (1) about 132 (141–170), long, nearly two-thirds of total length, origin behind origin of anal fin; anal about 139 (127–162), longer than dorsal, about three-quarters of total length, origin immediately behind anus; pelvics absent; pectorals small; caudal 6 (7), small. Branchiostegals 7. Lateral line not observed. Scales: absent. Colour, head and body dark, mouth and gill cavity black; peritoneum dark.

Length to 16 inches (40.6 cm).

Range: Pacific and Indian oceans. In the eastern Pacific reported from the Gulf of Panama and northern British Columbia.

The specimen was somewhat damaged, the skin eroded, the tail broken, and the anterior tips of the jaws missing. The following measurements were taken: total length 424 mm, caudal tip to anal fin origin 311 mm, caudal tip to dorsal fin origin 268 mm; head length 78.8 mm; mandibular length 38.2 mm; upper jaw length 31.6 mm; body depth 10.4 mm; head depth 11.4 mm; eye diameter 4.2 mm; caudal fin length 1.7 mm. As the anterior ends of the jaws are missing, the measurements of the jaws, head, and total length are incomplete. There may be about 3 mm missing from the upper jaw and 9 mm from the lower.

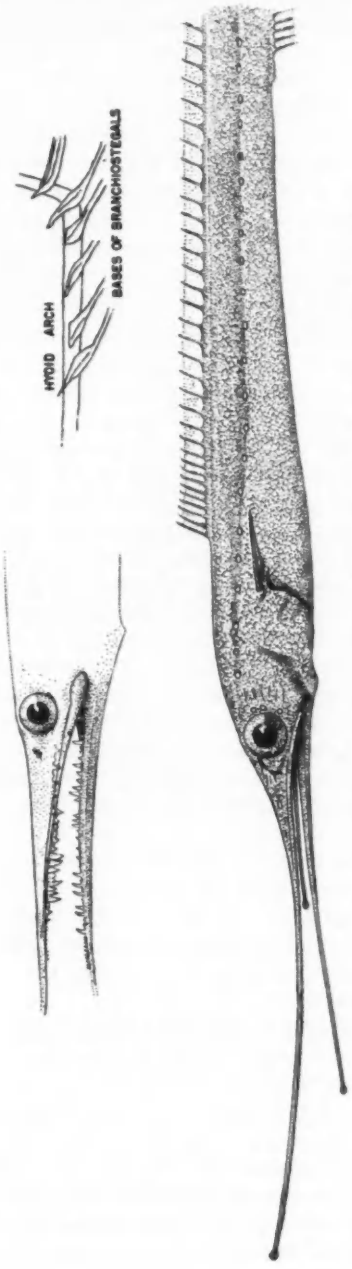

FIG. 2. *Top*, head and hyoid arch of *Serrivomer jesperseni*; *bottom*, head and trunk of *Avocettina infans*.

This specimen was compared with the descriptions in the latest revision of the genus by Bauchot (1959) and in Bauchot-Boutin (1953, 1954). It is clearly distinct from the all species described except *Serrivomer jesperseni*. It agrees with this species in dentition type, anal and caudal fin ray counts, and number and arrangement of the branchiostegals. It disagrees in that it has 132 instead of 147–170 dorsal rays. All previous specimens have been taken in tropical waters south of 25°N latitude. As a result of the cooler water of the North Pacific an increase in meristic count might have been expected rather than a decrease. Although Bauchot (1959) uses differences in vertebral number and fin ray counts to distinguish species, it does not seem wise to give taxonomic recognition to a single damaged specimen. The specimen is therefore referred provisionally to *Serrivomer jesperseni*.

CARISTIIDAE

Caristius macropus (Bellotti, 1903)

A single specimen was taken in a haul at 265–280 m 50 nautical miles southwest of Tasu Sound, Queen Charlotte Islands (52°17′N, 133°10′W) on July 10, 1965. The specimen, somewhat damaged on the top of the head is in collection No. BC65-627 of the Institute of Fisheries. This is the second specimen recorded from British Columbia and the northeastern Pacific. The first specimen was taken in 210 fath (384 m) south-southwest of Esteban Point on Vancouver Island in 1954 (Welander et al., 1957).

In the description below, the figures in parentheses are for the other known specimens of this genus as given by the above authors. Proportions are in thousandths of standard length.

Body ovate, compressed, deep, depth 470 (427–630). Head 306 (243–415), short, blunt, deep; mouth terminal, oblique; teeth, small slender, on jaws, vomer, and palatines, those on jaws uniserial except on tip of lower jaw where these are 3 irregular rows. Gill rakers, short, stout, 6 + 15 (5 + 14 to 6 + 16) on first gill arch. Snout blunt; eye large, diameter 98 (95–195). Caudal peduncle short, 145 (107–173). Fins: dorsal (1) more than 32 (III, 28 to 0, 34), first several elements lost; anal I, 21 (II, 16 to 0, 23), longest ray 227 (247–416), pelvics I, 5 (I, 5), thoracic, greatly elongate, longest ray 847 (434–697); pectoral 17 (17–19) first and last rays unbranched, longest ray 266 (227–353); caudal 18 (I, 17, I), rounded, longest ray 256 (170–331). Lateral line, very indistinct. Scales: cycloid, small, irregular in size and arrangement. Colour, uniform greyish brown.

Length to 12.3 inches (31.2 cm).

Range: British Columbia, Japan, the Azores, West Africa, Gibraltar, and Greenland.

The present specimen agrees well in nearly all respects with the descriptions for this species. There appears to be some confusion over the presence or absence of spines in the dorsal and anal fins. In this specimen the first element of the anal fin was a spine. The first part of the dorsal fin was too damaged to

determine whether or not a spine was present. In the other British Columbia specimen no spines were reported as the anterior part of both these fins was damaged. Attention might also be called to the fact that scales although generally small were irregular in size as well as arrangement.

ONEIRODIDAE

Oneirodes eschrichti-group (Bertelsen, 1951)

One specimen was taken in a haul at 52°11′N, 133°11′W (about 50 nautical miles southwest of Tasu Sound) on July 11, 1965, from a depth of 510–595 m. This the second record of a representative of this species-group from British Columbia. The specimen, 45.5 mm in standard length, is in collection No. BC65-623 of the Institute of Fisheries. It had suffered some damage to the skin, particularly on the head.

Body short, deep, broad and nearly globular; caudal peduncle short. Head large, broad; mouth terminal, very large, extending to just behind the eye. Teeth long, slender, depressible, on upper jaw 15, on lower jaw 19, 3 in a patch on each side of vomer, and in patches on the two pairs of upper pharyngeals. Eyes very small. Interorbital space deeply concave to base of illicium Spines: sphenotic spine (1) above and behind eye; articular spine (1) at posterior angle of jaw, quadrate element longer than mandibular. A broad, flat, triangular spine below articular, projecting downward at posterioventral corner of opercular apparatus. The opercular bone (Fig. 3, *right*) is strongly bifurcated,

Fig. 3. *Left*, opercular and subopercular bones of *Oneirodes acanthias*; *right*, opercular and subopercular bones of *Oneirodes eschrichti*-group.

the upper element about half the length of the lower, the suboperculum is pear-shaped. Symphyseal knob well developed. Gill membranes joined to body, gill opening small, below and behind pectoral fin. Fins: dorsal (1), 6, far back on body, directed backward; anal, 4, similar to dorsal; pelvics absent; pectoral 15 or 16; caudal 9, (2 unbranched, 4 branched, and 3 unbranched),

large, fan shaped. On the midline, halfway between sphenotic spine and dorsal fin is a short skin-papilla or "tubercle." Illicium (11.0 mm), about ¼ length of fish; basal bone (10.4 mm) long, extending beyond snout; esca 2.5 mm (5.0 mm including filaments). Esca: (Fig. 4, *right*) on the median line — anterior appendage digitiform, bearing short filaments on tip; symetrically placed tufts of

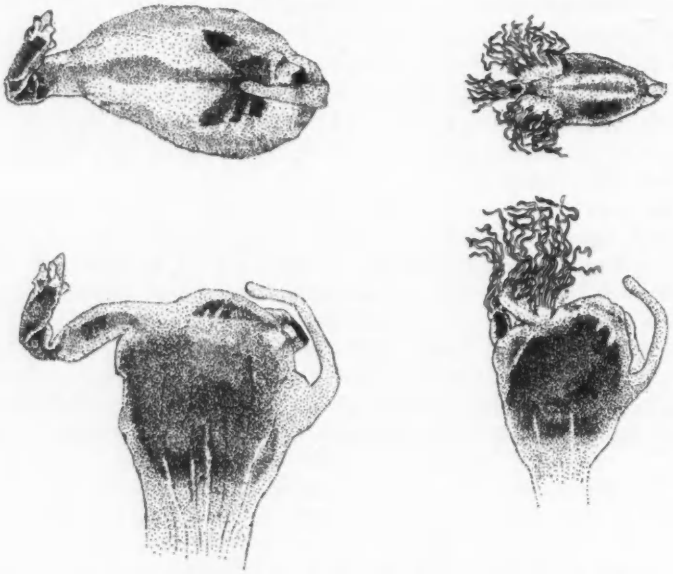

FIG. 4. *Left*, top and side views of the esca of *Oneirodes acanthias*; *right*, top and side views of the esca of *Oneirodes eschrichti*-group.

branching and rebranching filaments about twice length of anterior appendage; a truncated backward directed papilla; a posterior appendage, long, slender, curving forward over papilla. A small patch of fine filaments on the upper surface below median tufts of filaments. Esca generally well pigmented with pigment intensifying in anterior appendage and papilla.

Length to 8.9 inches (22.7 mm).

Range: Pacific, Indian, and Atlantic oceans. In the northeastern Pacific from the Gulf of Panama and northern British Columbia.

Bertelsen (1951) grouped together a number of species of *Oneirodes* and *Dolopichthys* as the *Oneirodes eschrichti*-group pending the collection of more specimens. In this group he placed *O. bulbosus* Chapman 1939, the only ceratioid previously reported from British Columbia. The single specimen was taken in much the same area as the one described here. Our specimen agrees well with Chapman's (1939) description — the form of the esca in particular is very similar. However, the numbers of dorsal, pectoral, and caudal fin rays,

and numbers of teeth in the upper and lower jaws differ from Chapman's specimen, but remain within the ranges given for the *O. eschrichti*-group. Chapman's specimen had 5 dorsal rays, 13 pectoral rays, 8 caudal rays, 12 teeth in the upper jaw and 11 in the lower. Bertelsen gives ranges for the fin rays as dorsal 5–7, pectoral 13–19, and caudal 9; he does not mention the number of teeth.

ONEIRODES ACANTHIAS (GILBERT, 1915)

A single specimen most probably of this species was caught in the same haul as the specimen of the *O. eschrichti*-group, i.e. from 510–595 m at 52°11′N, 133°11′W, on July 11, 1965. It is the first record of this species from British Columbia. The specimen which suffered some damage to the skin of the head is in collection No. BC65-623 of the Institute of Fisheries. The fish was 56.0 mm in standard length.

Body short, deep, broad and nearly globular; caudal peduncle short. Head large, broad; mouth terminal, very large, extending to just behind the eye. Teeth long, slender and depressible, in upper jaw 13, in lower 15, 3 in patches on each side of vomer and in patches on the two pairs of upper pharyngeals. Eye very small; interorbital space deeply concave to base of illicium.

Spines: sphenotic (1) above and behind eye; articular spine (1), quadrate element longer than mandibular; broad flat triangular downward projecting spine at the posterior corner of the opercular apparatus. The opercular bone (Fig. 3, *left*) is strongly bifurcated and similar in appearance to that of the specimen of the *eschrichti*-group; the suboperculum instead of being pear shaped is more slender and somewhat club shaped. The symphyseal knob is only weakly developed. The gill membranes joined to the body; gill opening small, below and behind pectoral fins. Fins: dorsal (1), 6, far back on body, directed backward; anal 4, similar to dorsal; pelvics absent; pectorals 15; caudal 9, (2 unbranched, 4 branched, and 3 unbranched), large, fan shaped. On the midline, halfway between sphenotic spines and dorsal fin a short skin-papilla or "tubercle." Illicium: on snout about one-fifth length of fish; basal bone (5.6 mm) short, not extending beyond snout. Esca (3.1 mm) with anterior digitiform appendage bearing short, stout processes on tip; no filament tufts on median line; papilla short, truncated, directed posteriorly; posterior appendage simple, slender, curved forward over papilla (Fig. 4, *left*); a tuft of fine filaments on the upper third of lateral surface just anterior to but below papilla. The body of the esca is well pigmented; dense pigmentation extends from the tip of the anterior appendage posteriorly, contracting mesially and then expanding into short birdlike wings immediately before the papilla, which bears a heavily pigmented median stripe. The posterior appendage is unpigmented.

Length to 3.1 inches (8.0 cm)

Range: Eastern Pacific. California to Alaska.

Bertelsen (1951) synonymises *Dolopichthys thompsoni* Schultz, 1934, with *Oneirodes acanthias* (Gilbert) 1915 because of similarity in the form of the esca.

Both were described from single specimens, *O. acanthias* (Gilbert) from California and *D. thompsoni* Schultz from the Gulf of Alaska. Bertelsen reports that two additional specimens were taken by the Crocker-Stanford expedition off California (at 33°11′N, 118°20′W). The specimen described here agrees with *O. acanthias* in the size of the illicium, in the form of the esca, in the number of teeth on dentary (15 in Gilbert's type, 18 in *D. thompsoni*) and in the form of the articular spines. The shape of the opercular and subopercular bones has not previously been described. A dorsal pore had not been observed previously in this species.

Chaenophryne cf. *parviconus* Regan and Trewavas, 1932

The damaged, skinned head of a ceratioid was found in one haul at 51°-26′N, 131°09′W, 30 nautical miles south by west of Cape St. James, at a depth of 730–825 m. From it the following measurements were made: head length (snout to opercular tip) 48.3 mm; head depth 41.4 mm; upper jaw 33.0 mm; lower jaw 44.4 mm; illicial bone (remaining length) 120 mm; eye diameter about 3 mm; longest tooth in lower jaw 7.1 mm. There were well-developed, slender canine teeth on the jaws, in two patches on the vomer and on the two pairs of upper pharyngeals. Gill rakers absent. Five of the 7 branchiostegals were on the ceratohyal, one on the border between it and the epihyal; the 4 upper were on the external face, the 2 lower on the ventral. The buccal cavity was black and judging from the remnants of skin, the head black.

The shape of the operculum and suboperculum is quite different from the other ceratioids known to occur in British Columbia (genus *Oneirodes*) and agrees closely with the shape of those in genus *Chaenophryne*. The diagnostic features for identifying to species are missing. On geographic grounds it would appear likely to be *C. parviconus*. This species is known from Oregon (Grinols, MS, 1965, 1966) and from the Atlantic, Indian, southern and eastern Pacific oceans including the Gulf of Panama (Bertelsen, 1951).

The specimen is in collection No. NMC65-26, of the National Museum of Canada.

ACKNOWLEDGMENTS

I would like to express my thanks to Dr D. E. McAllister of the National Museum of Canada; Mrs Isabel Radforth of the Royal Ontario Museum; and the staff of the Institute of Fisheries of the University of British Columbia for all the help they have given.

REFERENCES

Aron, Wm. 1960. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. Univ. Washington, Dept. Oceanog. Tech. Rept. No. 63. p. 1–65, appendices a3 to a156.

Bauchot, M. L. 1959. Etude des larves léptocephales du groupe *Leptocephalus lanceolatus* Stromann et identification à la famille des Serrivomeridae. Dana Rept., **48**: 1–148, 2 pl., 105 fig.

BAUCHOT-BOUTIN, M. L. 1953. Révision synoptique du genre *Serrivomer*. Bull. Museum Natl. Hist. Nat., Ser. 2, **25**: 365–367, 4 fig.
1954. Identification de *Serrivomer beani* Gill et Ryder (teleostéen anguilliforme). Ibid., **26**: 303–306, 2 fig.

BERTELSEN, E. 1951. The ceratioid fishes. Ontegeny, taxonomy, distribution and biology. Dana Rept., **39**: 1–276, 1 pl., 141 fig.

CHAPMAN, W. M. 1939. Eleven new species and three new genera of oceanic fishes collected by the International Fisheries Commission from the northeastern Pacific. Proc. U.S. Natl. Museum, **86**(3062): 501–542, 70 fig.
1940. Oceanic fishes from the northeast Pacific Ocean. B.C. Provincial Museum Occasional Papers, **2**: 1–40.

CLEMENS, W. A., AND G. V. WILBY. 1961. Fishes of the Pacific coast of Canada. Bull. Fish. Res. Bd. Canada, No. 68. 2nd ed. 443 p.

COHEN, D. M. MS, 1957. Contribution to a classification of fishes of the suborder Opisthoproctoidei. Ph.D. Thesis. Stanford Univ. 294 p., 6 fig.
1958. *Nansenia candida*, a new species of argentinid from the North Pacific, with notes on other species of Nansenia. Stanford Ichthyol. Bull., **7**(3): 52–57, 1 fig.

GRINOLS, R. B. MS, 1965. Check-list of the offshore marine fishes occurring in the northeastern Pacific Ocean, principally off the coasts of British Columbia, Washington, and Oregon. Univ. Washington, College of Fisheries. 217 p.
1966. Addition of adult anglerfish *Chaenophryne parviconus* Regan and Trewavas (Pisces: Oneirodidae) to the eastern subarctic Pacific Ocean. Calif. Fish Game, **52**(3): 161–165.

HARRY, R. R. 1951. Deep sea fishes of the Bermuda oceanographic expedition. Family Paralepididae. Zoologica, **36**(1): 17–35, 9 fig.
1953. Studies on the bathypelagic fishes of the family Paralepididae. 1. Survey of the genera. Pacific Sci., **7**(2): 219–249, 22 text-fig.

LAVENBERG, R., AND R. GRINOLS. MS, 1965. A review of *Sagamichthys abei* Parr from the Pacific Ocean. Los Angeles County Museum.

MARSHALL, N. B. 1966. Family Scopelosauridae. *In* Fishes of the Western North Atlantic. Mem. Sears Found. Marine Res., **1**(5): 194–204. fig. 50–54.

MEAD, G. W., AND F. H. C. TAYLOR. 1953. A collection of oceanic fishes from off northeastern Japan. J. Fish. Res. Bd. Canada, **10**(8): 560–582, 8 fig.

MCALLISTER, D. E. 1959. A collection of oceanic fishes from off British Columbia, with a discussion of the evolution of black peritoneum. Bull. Natl. Museum Canada, **171**: 39–43

PEDEN, ALEX E. 1966. Rare marine fishes from British Columbia with first records of silver perch, *Hyperprosopon ellipticum*, shanny, *Leptoclinus maculatus*. J. Fish. Res. Bd. Canada, **23**(8): 1277–1280.

ROFEN, R. R. 1966. Family Paralepididae. *In* Fishes of the western North Atlantic. Mem. Sears Found. Marine Res., **1**(5): 205–461, fig. 55–162.

ROULE, L., AND L. BERTIN. 1929. Les poissons Apodes appartenant au sous-ordre des Nemichthydiformes. Dana Rept., **4**: 1–113, 9 pl., 57 fig.

SCHÄRFE, J. 1960. A new method for "aimed" one-boat trawling in midwater and on the bottom. FAO Studies Rev. Gen. Fish. Council Mediterranean, **13**: 1–38, 32 fig.

SCHULTZ, L. P. 1934. A new ceratiid fish from the Gulf of Alaska. Copeia, 1934(2): 66–68, 1 fig.

TAYLOR, F. H. C. 1967a. Midwater trawl catches from Queen Charlotte Sound and the open ocean adjacent to the Queen Charlotte Islands. Fish. Res. Bd. Canada, Tech. Rept. No. 11: 1–39, 5 fig.
1967b. The relationship of midwater trawl catches to sound scattering layers off the coast of northern British Columbia. J. Fish. Res. Bd. Canada. (Submitted for publication.)

WELANDER, A. D., D. L. ALVERSON, AND P. BERGMAN. 1957. Rare fishes from the eastern North Pacific Ocean. Wash. Dept. Fish., **2**(1): 60–66, 2 fig.

WHITLEY, G. P. 1931. New names for Australian fishes. Australian Zool. Sydney, **6**: 310–334, pl. XXV–XXVII, 1 text fig.

The White Sucker Population of South Bay, Lake Huron, and Effects of the Sea Lamprey on It[1,2]

By Daniel W. Coble[3]

Ontario Department of Lands and Forests
Glenora Fisheries Station, Picton, Ont.

ABSTRACT

Information on ecology and dynamics of white suckers, *Catostomus commersoni* (Lacépède), in South Bay, Lake Huron, was obtained from experimental fishing over more than a decade and from a tagging program in 1955 and 1956. (A total of 1667 suckers were tagged and 8% of them were subsequently recovered.) The fish moved about extensively in the bay, minimal distance travelled averaging 3.8 km during a summer. Nevertheless, it was necessary to divide the bay into discrete fishing areas for calculating population and mortality estimates. The length–weight relationship of adult suckers in June was $W = 5.883 \times 10^{-4} L^{2.92262}$, where W is weight in pounds and L is fork length in inches. Growth averaged only about 7.6 mm/year, and an annulus was not formed on the scales every year. In 1956 the population may have amounted to about 160,000 adult white suckers, or 23 fish per hectare or 17.5 kg/hectare, for the part of the bay less than 36 m deep. The exploitation rate appeared to be less than 2%. The annual survival rate of suckers larger than approximately 38 cm appeared to be about 70–75% decreasing with size of fish. Although it is not known if the size of the population has changed, the size composition changed between 1953 and 1964 through the loss of larger fish. Marked changes in the fauna of South Bay subsequent to the late 1940's include the invasion of the sea lamprey, *Petromyzon marinus* Linnaeus, and the alewife, *Alosa pseudoharengus* (Wilson), the disappearance of the lake trout, *Salvelinus namaycush* (Walbaum), and the decline of the population of the cisco, *Coregonus* (= *Leucichthys*) *artedii* LeSueur. The loss of the larger fish in the white sucker population was probably caused by the sea lamprey, for it occurred after the destruction of the lake trout population and corresponded with increased incidence of lamprey scarring of suckers.

RÉSUMÉ

Des renseignements concernant *Catostomus commersoni* (Lacépède) à la Baie Sud, Lac Huron, obtenus par un programme d'étiquettes et par la pêche expérimentale depuis plus d'une décade sont présentés. En 1955 et 1956 un total de 1667 *C. commersoni* furent marqués 8% desquels furent retrouvés par la suite. Le poisson parcourut de vastes distances dans la baie, la distance minimale donnât une moyenne de 3.8 km au cours d'un été. Il fût nécessaire, quand même, de diviser la baie dans des régions de pêche discrètes pour calculer la population et l'évaluation de la mortalité. La relation de longueur et de poids chez les adultes de *C. commersoni* au mois de Juin était $W = 5.883 \times 10^{-4} L^{2.92262}$; W représente le poids en livres et L représente la longueur de la fourche de la queue en pouces. La pousse annuelle ne donnait qu'une moyenne de ca. 7.6 mm/an, et un annulus ne fût pas formé sur les écailles chaque année. En 1956 la population des adultes de *C. commersoni* pût amonter à ca. 160,000, ou 23 poissons par hectare, ou 17.5 kg/hectare pour les parties de la baie moins que 36 m de profondeur. Il semblât, que les poissons

[1]Received for publication March 28, 1967.
[2]Contribution No. 67-10 of the Ontario Department of Lands and Forests, Research Branch, Maple, Ontario.
[3]Present address: Missouri Coop. Fish. Unit, Stephans Hall, Univ. Missouri, Columbia, Mo. 65202.

J. Fish. Res. Bd. Canada, **24**(10), 1967.
Printed in Canada.

furent soumis à un degré d'exploitation de moins de 2% et un pourcentage annuel de survivance de ca. 70–75% diminuât avec la grosseur des poissons. Bien qu'on ne sache pas, si la dimension de la population de *C. commersoni* aît changée, la composition des grosseurs a changée depuis 1953 par la perte des plus gros poissons. Des changements marqués dans la faune de la Baie Sud vers la fin de 1940, l'invasion de *Petromyzon marinus* Linnaeus, et de *Alosa pseudoharengus* (Wilson) et la disparition de la population de *Salvelinus namaycush* (Walbaum) et la baisse de la population de *Coregonus* (= *Leucichthys*) *artedii* LeSueur sont compris. La perte des plus gros poissons de la population de *C. commersoni* fût dû probablement à la déprédation de *P. marinus*, parce qu'elle eût lieu après la destruction de la population de *S. namaycush* et parce qu'il y eût correspondance avec les incidences augmentées des cicatrices de *P. marinus* aux *C. commersoni*.

INTRODUCTION

DATA ON white suckers, *Catostomus commersoni* (Lacépède), obtained from an experimental fishery in South Bay, Lake Huron, from 1947 to 1964 and from a tagging program in 1955 and 1956 were analysed to obtain information on the ecology and dynamics of the species and on possible effects of the sea lamprey, *Petromyzon marinus* Linnaeus, on the population.

Information from tagging includes data on movements and growth, estimates of population size and exploitation, and mortality rates. Information from the experimental fishery includes sizes of catches of white suckers, alewives, *Alosa pseudoharengus* (Wilson), and ciscos, *Coregonus* (= *Leucichthys*) *artedii* LeSueur, in various years and data on the size composition and lamprey scarred proportions of catches of suckers in various years. This information along with earlier work on lake trout, *Salvelinus namaycush* (Walbaum), in South Bay described by Fry (1952) indicates that the sea lamprey has affected the size composition of the sucker population, but may or may not have altered the size of the population.

South Bay (45°35'N; 82°W) is a 22.5 km long arm of Lake Huron extending into the southeast corner of Manitoulin Island (Fig. 1). About one-quarter of the way up the bay from its narrow 200 m-wide entrance, a constriction of about 1.2 km divides the bay into two basins. The outer basin with a maximum depth of about 12 m comprises 16%, and the inner basin with a maximum depth of about 55 m comprises 84% of the 85.5 km² area of the bay.

DATA AND METHODS

Information presented here was taken from catch and sample data from experimental fishing for various species of fish with various kinds of commercial gear in South Bay from 1947 to 1964. Most of the data were from catches in pound nets (Lagler, 1956) but also included information from catches in hoop nets, trap nets, and gill nets. Much of the pound net effort involved fishing the same nets in the same locations in the outer basin year after year (Fig. 1). Stretched mesh size in the pot of 1-pound net (No. 6) was 3 inches, in two others it was 1½, and in the other two nets, 1 inch. Most of the trap, hoop, and gill netting was conducted in the inner basin, and the locations of sets and the mesh sizes varied widely.

Except when fish were released, after counting and usually after marking, catches were taken to the South Bay Fisheries Research Station. For each

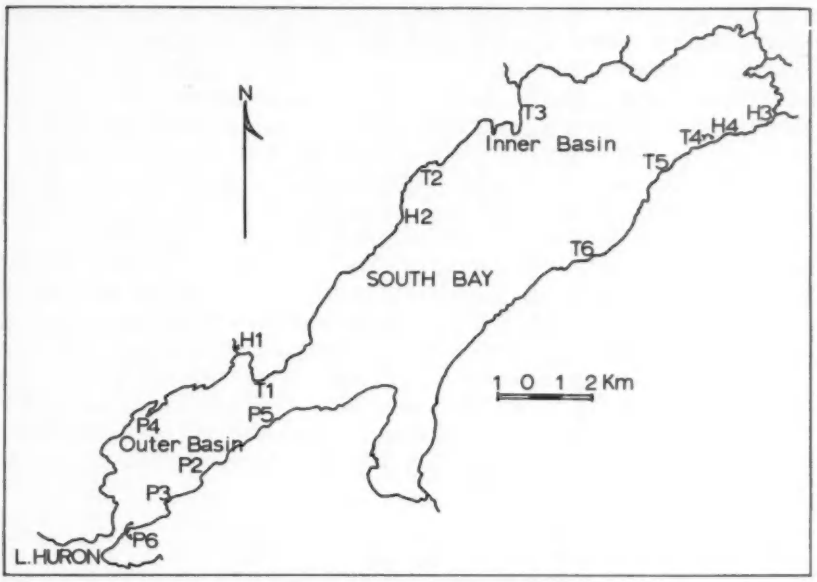

FIG. 1. South Bay, showing locations of various pound nets (P), trap nets (T), and hoop nets (H) in 1956. There is no P1.

catch the number and weight of each species were recorded. In large catches a sample of each species was taken; in smaller ones the catch itself comprised the sample. For each fish in a sample, scales were taken and length, weight, sex, state of maturity, presence of lamprey marks or fin clips, and other anomalies were recorded. From 1960 to 1964 sample sizes for large catches were 20 individuals of each species in each catch; earlier sample sizes were smaller.

In 1955, 76 white suckers were tagged and in 1956, 1591 were tagged. In total 8% of them were subsequently recovered. At tagging the fish were lightly anesthetized in approximately 5% urethane solution, were measured to the nearest half inch, fin clipped, and tagged; and a scale sample was taken. An oval tag, 12.7 by 7.6 mm of yellow celluloid, was attached through the musculature at the anterior base of the dorsal fin with 6-pound test monofilament nylon line (Fraser, 1955). The mean of 100 fork lengths chosen at random from those recorded from suckers tagged in 1956 was 15.2 inches (38.6 cm), and the standard deviation, 1.8 inches (4.6 cm). In 1956 suckers were tagged from catches in impounding gear operated in the locations shown in Fig. 1. The periods of time that the nets were fished and the number of suckers tagged from each are given in Table I. In 1955, 65 of the 76 white suckers tagged were captured and released in early June at sites designated as T4 and T5 in Fig. 1.

The data on the tagged fish were analysed in the light of three types of possible systematic errors (Ricker, 1958) in an attempt to detect any indication

TABLE I. Dates that various impounding nets were operated in South Bay, Lake Huron, in 1956, and numbers of white suckers tagged and released from each.

Pound net	Date	No. tagged	Hoop net	Date	No. tagged	Trap net	Date	No. tagged
2	May 28–July 16	96	1	Apr. 25–Apr. 30	51	1	July 3–Aug. 2	18
3	May 28–Aug. 3	184	2	June 8–July 10	20	2	June 6–Aug. 6	50
4	May 18–July 24	98	3	June 8–July 10	12	3	May 18–July 10	290
5	May 28–July 18	216	4	June 12–July 10	1	4	June 6–Aug. 6	143
6	June 4–July 25	26				5	June 26–Aug. 1	316
						6	June 26–Aug. 2	70
	Total	620		Total	84		Total	887

of biases. Type A errors include incomplete reporting of recaptures, tag loss, mortalities occurring shortly after handling. Type B errors include continued tag loss or mortality due to tagging throughout the study period, and emigration from the fishing area. Type C errors include abnormal behaviour of marked fish and non-random distribution of tagged fish or fishing effort.

There is not much direct evidence concerning Type A errors in the data, but all available evidence indicated that these errors were not important. It is doubtful that there was incomplete reporting of tags. Suckers were caught by the experimental fishing gear by staff associated with the fishing program. Since all suckers in a catch were either tagged and released or taken ashore and counted, few recoveries of tagged fish could go undetected. There is no evidence of tag loss or short-term handling mortalities. In 1955, three tagged suckers were put back in a pound net, and after 3 days none had died or lost tags. In 1965, 30 yellow perch tagged in the same manner as the suckers were released in pound nets. After 4 days no dead ones were found and there was no evidence of tag loss. Some of both species did escape from the nets. Through the years several other species, totaling well over 10,000 fish, have been tagged

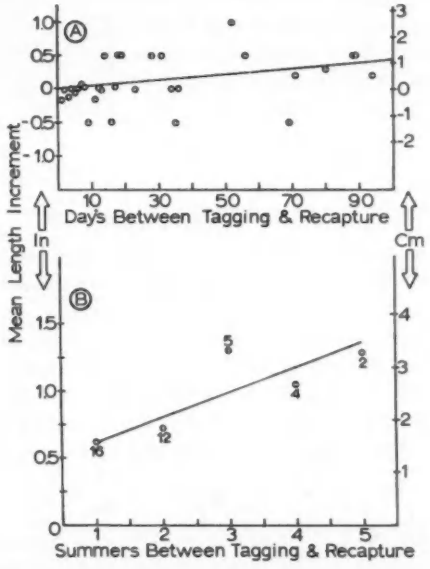

FIG. 2. A, mean length increments of 85 tagged white suckers in South Bay in the summer of 1956. Regression line placed by the method of least squares. B, mean length increments of 39 tagged white suckers in South Bay over a period of 5 years. Number beside each point represents the number of fish recaptured. Regression line placed by the method of least squares.

in the same manner as white suckers. No evidence has been found that these errors may be important.

The little evidence available indicates that Type B errors were not of importance. Since fish were fin clipped at time of tagging, tag loss can be identified by recapture of fish bearing a fin clip but no tag. In August 1956, several weeks after most of the fish were tagged, 616 white suckers were taken in gill nets. The catch included six recaptures and 268 of the suckers were sampled, i.e. individually scrutinized. A catch of 413 suckers in pound nets the following June included eight recaptures and 275 of the fish were sampled. None of the 543 sampled suckers were found to be fin clipped. Similar results have been obtained for yellow perch in South Bay.

If there were mortality due to tagging, then exploitation rates calculated from recapture data would decrease with time, and mortality rates calculated from such data would be higher than those obtained from other information. Data presented below indicate that there was no apparent decrease in exploitation rate from 10 to 100 days after tagging (Fig. 3), and mortality rates determined from a catch curve were similar to those calculated from tagged fish.

There is no evidence of important emigration of white suckers from South Bay. Only one tagged sucker was reported from outside, and it is likely that more would have been reported if there were substantial movement of white suckers out of the bay. Budd (1956) found an extensive movement of lake whitefish out of South Bay.

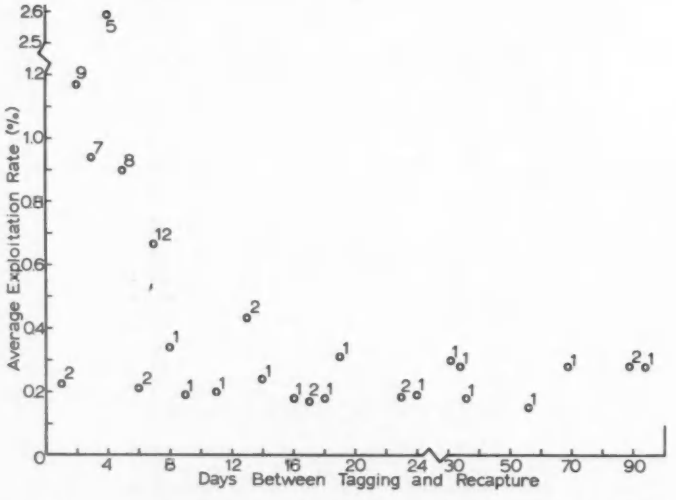

FIG. 3. Average percentage exploitation rates (number of fish recaptured multiplied by 100 and divided by the number of tagged fish available) in relation to time between tagging and recapture. Number beside each point indicates the number of fish recaptured. There is a change in scale in the latter part of the abscissa.

The recapture data probably were affected by one source of Type C error, non-random distribution of marked fish among the population. There was an abnormally high exploitation rate in the 1st week after tagging (Fig. 3), which indicates that the marked fish were not randomly distributed among the population then. The data concerning this source of error are considered below along with the population estimates. No indication of abnormal behaviour of tagged suckers, a second source of Type C error, was noted. The amount of movement seemed to be the same 2 months after tagging as immediately after tagging (Table II).

TABLE II. Minimal distances travelled by white suckers in various periods of time in South Bay in 1956.

Days between tagging and recapture	Mean minimal distance travelled (*km*)	*n*	Days Between tagging and recapture	Mean minimal distance travelled (*km*)	*n*
1	4.8	2	10	4.7	4
2	0.6	11	16	4.3	9
3	1.9	7	22	2.7	3
4	5.1	7	33	5.6	6
5	3.1	10	52	12.9	2
6	8.0	5	56	1.0	1
7	3.4	13			
Mean				3.8	80

THE WHITE SUCKER POPULATION

White suckers inhabit both basins of South Bay and occur commonly in catches of all of the different kinds of fishing gear. They make up a substantial proportion of catches in gill nets of graded mesh sizes extending from 1 to 6 inches stretched measure. Unpublished information on the depths at which they are caught in South Bay indicates that in the ice-free season they inhabit water less than about 36 m deep or about 70 km² of the bay. In spring they ascend tributaries to spawn, and it is not known if they spawn also in the bay itself. In South Bay they are not sought by anglers or commercial fishermen.

MOVEMENTS

The single marked sucker reported from outside South Bay was caught in 1961, 5 years after it was tagged, about 56 km away. For the remainder of the recaptures, analysis of data on movements was confined to those from fish recaptured in the year of tagging, and all movements were calculated as straight line distances. Average calculated distances travelled by 80 tagged suckers caught in impounding gear in 1956 ranged from 0.6 to 12.9 km, and the mean distance for all was 3.8 km (Table II). No relationship between distance travelled and time at large was evident.

To determine the effect of size on distance travelled, recapture data were divided into two groups, one of 53 suckers 15.5 inches or more in length, and one of 34 fish less than 15.5 inches in length. The mean distances travelled were 3.9 km for the large group and 3.7 for the small one. The tagging and recapture regimen allowed for analysis of movements of some fish in June and July separately. The average distance moved by 41 white suckers in June was 3.1 km and for 12 fish in July, 3.5 km; these means are not significantly different (t-test).

Olson and Scidmore (1963) also found that white suckers move about extensively. They found that suckers marked in a spawning area in spring in Many Point Lake, Minnesota, a lake of 7.1 km², dispersed widely by summer. However, these indications of extensive movement by suckers (more movement, for example, than has been reported for Centrarchids) do not necessarily indicate that the fish continuously roam throughout the body of water.

Closer inspection of the South Bay data indicated that there was restricted movement between different areas of the bay, and at any one time the population of the bay may not be one homogeneous group. Percentages of catches made up of fish tagged in one location in 1956 were compared between the tagging location and other areas of the bay (Table III). Of 1683 white suckers

TABLE III. Numbers of white suckers tagged in various locations in 1956 that were recaptured within 3 months in the same and other locations; catches in the various locations; and ratios of recaptures to catches during given periods of time. M indicates number tagged; C, number caught; R, number recaptured. Tagging continued from May 18–August 6.

Suckers tagged in inner basin (*May 18–August 6, M = 902*)

Location	C	R	R/C (%)
Inner basin	1683	28	1.7
Outer basin	1021	3	0.3

Suckers tagged in outer basin (*June 6–August 3, M = 689*)

Location	C	R	R/C (%)
Outer basin	657	17	2.6
Inner basin	1533	7	0.5

Suckers tagged in area 3 (*May 18–August 6, M = 542*)

Location	C	R	R/C (%)
Area 3	1285	18	1.4
Area 2	398	1	0.3

Suckers taggedat P2 (*May 18–August 3, M = 96*)

Location	C	R	R/C (%)
P2	104	1	1.0
P3	248	1	0.4
P4	135	1	0.7
P5	260	5	1.9
P6	35	0	0
T1	261	0	0

Suckers tagged at T4 (*May 18–July 12, M = 143*)

Location	C	R	R/C (%)
H3	16	1	6.2
H4	1	0	0
T4	167	2	1.2
T5	346	4	1.2
T6	277	2	0.7

caught in the inner basin, 28 fish, or 1.7%, had been tagged there. Of 1021 suckers captured in the outer basin during the same period, only three, or 0.3%, had been tagged in the inner basin. The difference in the recaptures, which is significant (chi-square test), indicates that within a period of about 3 months fish marked in the inner basin did not comprise the same percentage of the population in the outer basin as in the inner. Similar data for fish tagged in the outer basin indicated that fish marked there made up a different proportion of the population in that basin than in the other. Hence the data for each basin were treated separately for population and mortality estimates.

Further analysis of data from the inner basin indicated that it did not contain one homogeneous group of suckers. Within the inner basin there were two distinct fishing areas (Fig. 1). The one in the middle of the basin on the north side is here designated area 2 and the one on the south side near the east end is area 3; the outer basin is area 1. The data (Table III) indicate that within 3 months suckers tagged in area 3 made up a different proportion of the population there than in area 2. It appeared, therefore, that although the tagging information indicated that the fish moved about considerably, there was so little movement of suckers from one fishing area to another within a 3-month period that the data for each of the three areas should be treated separately for population and mortality estimates. There was enough movement between areas, however, that none of the areas could represent a genetically isolated population.

There was considerable movement of suckers within areas. Within areas 1 and 3 recaptures of fish tagged at P2 and T4 in relation to catches in all nets (Table III) were reasonably similar, and the suckers in each area were considered a single group.

Length–Weight Relationship

A length–weight relationship was calculated with data from samples of catches of white suckers in pound nets in June. A mean weight was calculated for each $\frac{1}{10}$-inch length interval between 10 and 18 inches inclusive, and also for suckers of 9.0 inches. All but four of these 82 average weights were calculated from 10 individual weights. The relationship then, is based on 811 white suckers from 9 through 18 inches. Most of the data were from fish taken in 1957 and 1958, and the rest for almost all other years from 1947 through 1964. The relationship may be expressed as

$$W = 5.883 \times 10^{-4} L^{2.92262}$$

or by the linear equation, $\log W = -3.2304 + 2.92262 \log L$, where W is weight in pounds and L is fork length in inches.

Growth of Tagged White Suckers

Adult white suckers in South Bay grow very slowly. The mean length increments of 85 white suckers tagged from April 25 to July 6, 1956, and

recaptured in the same year (Fig. 2A) indicated that growth amounted to less than half an inch (12.7 mm) for the summer. The 53 suckers that were 15.5 inches or more fork length did not grow faster or slower (F test) than the 32 fish less than 15.5 inches. Average increments of 39 suckers recaptured one or more summers after tagging (Fig. 2B) also showed a slow growth rate. The total increase in length was less than 1.5 inches (38.1 mm) after $4\frac{1}{2}$ years (5 summers). These data indicated that the average annual length increment of adult white suckers in South Bay was about 0.3 inches (7.6 mm).

Coble (MS, 1965) found that there was very little growth in normal adult white suckers in South Bay. Hence it is not likely that the slow growth of the tagged fish was attributable to the tags. Geen et al. (1966) reported that adult white and longnose suckers, *Catostomus catostomus* (Forster), in Sixteenmile Lake, British Columbia, grew only 10–20 mm in a year.

A comparison of the number of annuli on scales of South Bay suckers taken at tagging and at recapture showed that an annulus was not formed every year. Ovchynnyk (1965) and Geen et al. (1966) also reported that white sucker scales did not provide a reliable index of age, as Dence (1948) had previously found for dwarf white suckers, *Catostomus commersonii utawana* Mather.

Size of Population, 1956, Exploitation Rates, and Mortality Rates

At least two different kinds of population estimates for 1956 were calculated from the tagging information for each of the three fishing areas in South Bay (Table IV). Schnabel estimates (Ricker, 1958, formula 3.21; Ricker, 1937) were made for each area from catches in impounding gear. Those given as Schnabel 1 in Table IV were calculated from all recaptures made during the period that suckers were tagged; those given as Schnabel 2 were calculated from fish at large more than a week. The reason that the second Schnabel estimates were calculated is given below.

Petersen estimates (Ricker, 1958, formula 3.7; Ricker, 1937) were obtained from catches made in impounding gear in areas 1 and 3 and gillnets in area 2 after the tagging period. A Parker population estimate (Ricker, 1958, p. 88) was made for area 1 from pound net catches. This estimate is obtained from the relationship to time of successive ratios of recaptures (R) to catches (C). In the data tabulated below, the logarithms of the R/C ratios decreased linearly.

Year	Catch	Recaptures
1957	423	5
1958	1772	6
1959	1489	2
1960+1961	2694	1

The population estimates fall into two size-ranges. In each area the Schnabel 1 estimate was a third or fourth as great as the corresponding Parker, Petersen, or Schnabel 2 estimate, indicating a bias in either the Schnabel 1

TABLE IV. Estimates, and data used in their calculation, of population sizes in 1956, exploitation rates, and annual survival rates of white suckers in three areas of South Bay, Lake Huron.

Estimate	Fishing period	Total no. caught	No. tagged	No. recaptured	$\hat{N}$	95% confidence interval of $\hat{N}$	Exploitation rate (%) with 95% confidence interval	Survival rate (%)
Area 1, outer basin								
Schnabel 1	Apr. 25–July 8, 1956	716	681	34	5,895			
Petersen	July 6–Aug. 2, 1956	299	689	5	34,450	17,667–129,187	0.2<0.7<1.7	60.0 Not weighted
Parker[a]	June, 1957–61	6,378	689	14	24,735	17,395–35,169	1.8	68.0 Weighted
Schnabel 2	Apr. 25–July 4, 1956	711	681	5	24,561	12,595–92,102		
Area 2, middle inner basin								
Schnabel 1	May 15–July 8, 1956	380	354	7	6,880			
Petersen	August, 1956	309	360	5	18,600	9,538–69,750	0.4<1.4<3.2	
Schnabel 2	May 18–July 5, 1956	395	340	2	13,738	5,724–206,065		
Area 3, end inner basin								
Schnabel 1	June 4–July 8, 1956	557	375	8	12,696			
Petersen	July 9–Aug. 6, 1956	728	542	10	35,920	21,474–84,068	0.9<1.8<3.4	75.8

[a]The 95% confidence intervals of the Parker estimate were calculated according to Snedecor (1956, p. 137).

or other estimates. A consideration of the conditions that must be satisfied for reasonably accurate population estimates from marking experiments indicated that the random distribution of marked fish in the population probably was not obtained in the 1st week after tagging.

Exploitation rates, the number of recaptures divided by the number of tagged fish available, were calculated for each area for each day after tagging on which a recapture was made. The data were pooled and a mean rate was calculated for the various days at large. Exploitation was higher in the 1st week after tagging than thereafter, when it was approximately constant (Fig. 3). A higher exploitation rate in the first week after tagging would affect estimates calculated from all mark and recapture data obtained during the period of tagging (Schnabel 1). Larger exploitation rates tend to reduce population estimates. It appears that the Schnabel 1 population estimates are biased and are too low. The second Schnabel estimates were calculated omitting mark and recapture data from suckers at large a week or less, in an attempt to eliminate bias caused by the unusually high exploitation rate in the 1st week at large.

The Parker, Petersen, and Schnabel 2 estimates given in Table IV may be approximately correct. They are all of the same order of magnitude and are in fairly good agreement within areas, even though they were obtained by different methods of calculation and from recaptures in two kinds of fishing gear or from the same gear in different periods of time. There is evidence that the essential requirement for reasonably accurate population estimates, negligible recruitment during the recovery period, was met. Because of the slow growth rate the number of suckers coming into the size-range exploited by the nets, say over 9 inches, must have been low. Furthermore, in area 1 the Parker estimate, which corrects for recruitment, was similar to the Petersen and Schnabel 2 estimates.

Nevertheless recaptures were few, and the confidence intervals of the population estimates large. Moreover, the reliability of confidence intervals calculated with parametric statistics from such ecological data is doubtful. It is questionable that they really are 95% confidence intervals. It seems best, therefore, to view the population estimates with reservation.

Areas 2 and 3 may each have been about equal to the size of the outer basin, area 1. If that be so, the three areas covered about half of the part of the bay shallower than 36 m and, perhaps, altogether contained about 80,000 adult white suckers, the sum of the estimates for each area with the smallest confidence interval. If there were as many white suckers in the half of the bay not covered by the nets, then there were about 160,000 adult white suckers in South Bay in the early summer of 1956. A like treatment of the 95% confidence intervals yields estimates of 100,000–380,000 suckers. If there were 70 km^2 of sucker habitat, there were 23 white suckers per hectare. Olson (1963) estimated 47 suckers per hectare for Many Point Lake, Minnesota, maximum depth 27.4 m. Geen et al. (1966) estimated 40 white suckers per hectare in Sixteenmile Lake, British Columbia, maximum depth 7.3 m. White

suckers caught in South Bay in 1956 averaged about 15 inches or 1.67 lb. A population of 23 fish per hectare would be about 17.5 kg per hectare.

It appears that the experimental fishing in South Bay caught a very small proportion of the population. Exploitation rates and their 95% confidence intervals were calculated for each area from some of the same data used to obtain Petersen population estimates (Ricker, 1958, p. 83; Ricker, 1937). The rates were 0.7% for area 1, 1.4% for area 2 and 1.8% for area 3 (Table IV). Another exploitation rate was calculated for area 1 from recapture data obtained from 1957 through 1961 and an estimated survival rate of 0.60 (Ricker, 1958, p. 112). The rate, 1.8% (Table IV), compares favorably with the estimates for areas 2 and 3.

Adult white suckers in South Bay seem to suffer a low annual mortality rate. Estimates of mortality rates were provided by two kinds of data: tagging information and a length-frequency distribution. Recaptures after 1956 in area 1 yielded a weighted estimate of survival of 0.68 and an unweighted estimate of 0.60 (Ricker, 1958, p. 111–112). A survival estimate of suckers tagged in 1955 in area 3 was 0.758 (Ricker, 1958, formula 5.2). These estimates are given in Table IV as percentage survival.

High rates of survival were also estimated from a catch curve. Since accurate data on ages of white suckers in South Bay were not available, it was not possible to construct the usual catch curve of frequency vs. age. Instead a length frequency was obtained from a total of 3120 fish from area 1. The numbers of white suckers in samples of catches from pound nets from 1957 through 1961 were tabulated in 11 1-inch length intervals from 10 to 20.9 inches (25.4–53.1 cm). Data for the 5 years were pooled and log frequencies plotted against the midpoints of the length intervals (Fig. 4).

In the descending right limb, changes in frequency were calculated by subtracting the log frequency corresponding to each point from the one immediately preceding it to yield in each case a decline in log units per inch. Each of these changes was multiplied by 0.3, the average annual length increment in inches of tagged suckers determined above, to obtain the change in frequency per year. These negative changes were written with a positive mantissa and antilogged to obtain the survival rate (Ricker, 1958, p. 44). For example, between 15.45 and 16.45 inches the frequency changed by −0.1766 log units per inch, or −0.05298 log units per year; the corresponding annual survival rate is 88.5%. Survival, of course, decreased throughout the remaining four intervals, and the rates were 78.4%, 75.2%, 57.2%, and finally 51.7% for suckers between 19.45 and 20.45 inches.

Ricker (1958, p. 73–74) cautions against the use of catch curves based on length frequencies because they yield biased estimates of survival unless the absolute increase in mean length of fish between successive ages is uniform over the range of ages corresponding to the lengths. It is not known if this condition was met in the white suckers. However, the fact that no difference in length increment between a group of large (15.5 inches or more) and a group of small tagged suckers could be demonstrated indicates that the con-

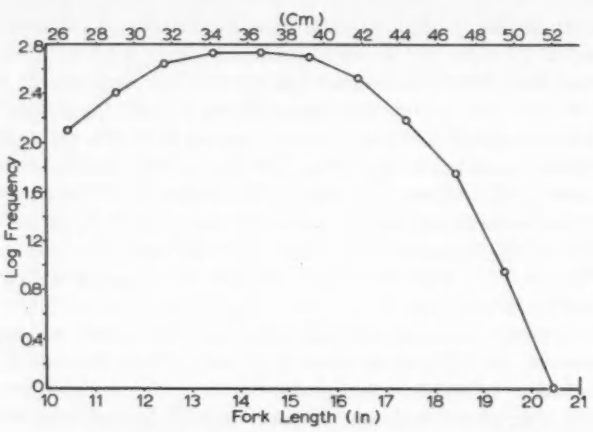

FIG. 4. Length-frequency curve of samples of white suckers in pound nets in South Bay in 1957 through 1961. The distribution was determined from a total of 3120 fish.

dition at least may have been approximated. If so, the estimates may be approximately correct.

Nevertheless, since the degree to which the condition was satisfied is not known, survival estimates from the catch curve probably should not be considered either more or less accurate than those obtained from tagged fish. The estimates from both sources were similar and indicate a low annual mortality rate in adult white suckers. The mean annual survival rate of six determinations, three from the catch curve for fish under 18.5 inches and three from tagged suckers, was 74.3%. Another conclusion, which is evident in the catch curve and is probably justified, is that the rate of mortality of fish larger than about 15 inches increased with size. Indications of a low mortality rate were also found by Geen et al. (1966) for adult white suckers in Sixteenmile Lake and by Dence (1948) for dwarf white suckers in Wolf Lake, New York. Olson (1963) estimated an annual survival rate of 86.9% for adult white suckers in Many Point Lake, Minnesota.

RELATIVE NUMBERS OF ADULTS, 1949–64

The relative size of the adult white sucker population in South Bay in various years may be reflected in the pound net catches. From 1949 through 1964, three pound nets, No. 2, 4, 5, were fished in the same locations every June. The total number of white suckers caught in the three nets in June of each year (Fig. 5) fell sharply after 1951 to a low point in 1953; then the catch increased, slowly at first, until by 1958 and subsequently it was at the same level or slightly higher than before 1952.

It is not known if the pound net catch is a reliable index of the size of the white sucker population. Budd and Fry (1960) presented evidence in-

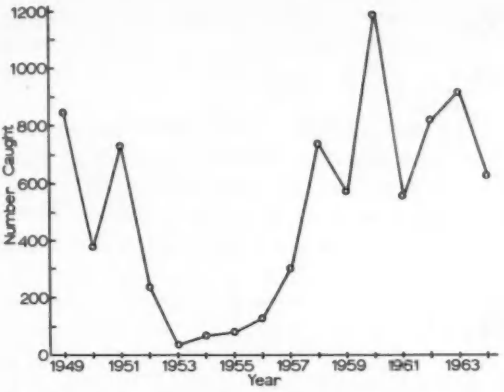

FIG. 5. Total numbers of white suckers in catches from pound nets 2, 4, and 5 in South Bay in June of various years.

dicating that it was for lake trout; they found a positive correlation between the catch per unit effort and estimated size of the population in different years. It would be desirable to have population estimates for white suckers for more years than just 1956 to compare with the pound net catches. If the pound net catch is a reliable index of the size of the sucker population, then the population estimate for 1956 is an estimate for the population when it was at a low point, lower than before 1952 and lower than after 1957.

SIZE COMPOSITION OF ADULT POPULATION, 1949–64

The pound net catches probably provide a good indication of the size composition of the adult sucker population. They provide evidence (Fig. 6) that the proportion of large fish in the population has decreased since around 1953. The average size of suckers in samples of pound net catches decreased through the years (Fig. 6A) because the proportions of large fish in the samples decreased (Fig. 6B).

SOME CHANGES IN THE FAUNA OF SOUTH BAY

Subsequent to 1947 there have been profound changes in the fauna of South Bay. Some newly arrived species have become prominent whereas some of the original inhabitants have declined or even disappeared. One of the important new additions to the fauna was the sea lamprey. The species was accurately reported to be in Lake Erie in 1921, and within the next 25 years it spread through lakes Huron, Michigan, and Superior (Scott, 1963). Adult lampreys attack large fish by attaching themselves to the fish with their sucker-like mouth, rasping a hole in the body wall, and sucking out blood and dissolved flesh. The sea lamprey decimated the lake trout populations in lakes Huron (Hile, 1946) and Michigan (Eschmeyer, 1955) and began to do the same to

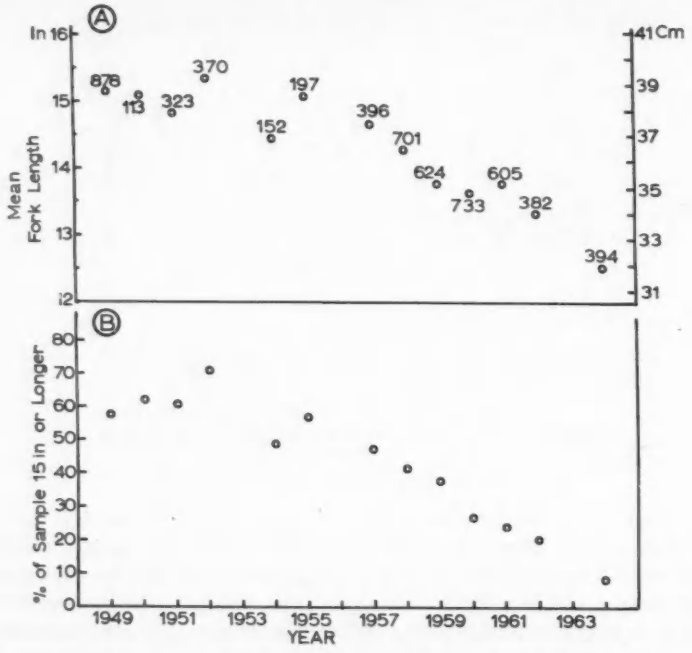

FIG. 6. A, mean lengths of samples of white suckers in catches in pound nets in South Bay in various years. Number beside each point represents the sample size. B, percentages of samples of white suckers in Fig. 6A that were 15 inches (38.1 cm) or longer.

those in Lake Superior before control measures were undertaken. Apparently the sea lamprey did not invade South Bay in sufficient numbers to affect the resident lake trout population until the late 1940's.

INVASION OF THE SEA LAMPREY AND EFFECT ON LAKE TROUT

Fry (1952) studied the South Bay lake trout population from 1947 to 1952. He reported the drastic decline of the population during those years. The population, which was estimated to consist of more than 20,000 adult trout in 1948, was virtually extinct in 1952. Throughout those years the incidence of lamprey scarring of trout increased markedly, particularly on the larger fish. The rate of reduction of the trout population was correlated with the incidence of lamprey marks, and the decline could not be attributed to human exploitation or to other causes such as diseases or catastrophic hydrological conditions. In subsequent work, marked yearling lake trout were planted in South Bay (Fry and Budd, 1957). Survival of the planted trout to age 4 was good, but the fish were eliminated by the sea lamprey before they could spawn (Budd and Fry, 1960).

It may be concluded that the sea lamprey was not present in numbers in South Bay before 1949, and that thereafter it destroyed the resident lake trout population, probably eliminating it completely in 1953.

Relative Sizes of Populations of Ciscos and Alewives, 1949–64

Catches in the experimental fishery in South Bay from 1949 through 1964 indicate that the cisco population declined drastically whereas alewives became tremendously abundant. Total weights of ciscos and alewives caught in pound nets in June in various years are shown in Fig. 7. The regularity

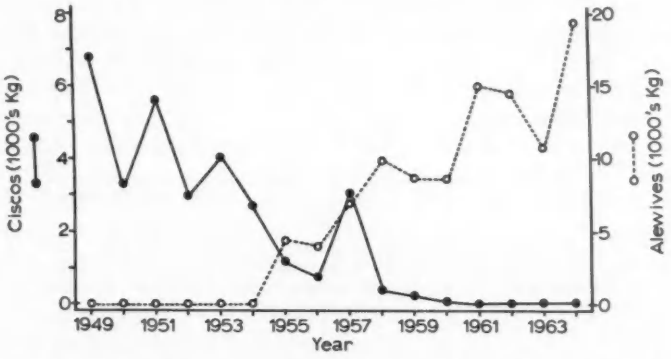

Fig. 7. Weights (thousands of kg) of ciscos and alewives in catches from pound nets in South Bay in June in various years. Catches of ciscos are total weights taken in nets 2, 4, 5. Catches of alewives are total weights taken in nets 2, 3, 4, 5; actually net 3 was not fished before 1952, but inclusion of data from that net in the first 3 years shown does not cause any error in the alewife catches because none were caught then.

of the data and observations in other areas of the Great Lakes indicate that these catches probably are reliable indications of relative sizes of the populations. The data indicate that the cisco population declined, irregularly at first, from 1949 to a very low level in 1960, which has been unchanged since. The cause(s) of the decrease is not known. The first alewife caught in South Bay was taken in 1951, and from 1954 the population increased rapidly to an extremely high level. Incidentally, the decline of ciscos appears to have been well under way before alewives were present in quantity (Fig. 7).

It does not seem appropriate to speculate on the possible effects of these changes on the sucker population. The changes are mentioned because they were of such magnitude that there can be no doubt that they affected the ecosystem of South Bay. As such, they could have influenced white suckers.

EFFECT OF THE SEA LAMPREY ON WHITE SUCKERS

The sea lamprey probably caused the change in the size composition of the white sucker population in South Bay shown in Fig. 6. Hall and Elliott

(1954) found that the percentage of white suckers in Lake Huron bearing lamprey scars increased as size of the suckers increased. For South Bay the percentage of white suckers 15 or more inches long bearing lamprey scars or wounds in samples of catches in June in various years in impounding gear are shown in Fig. 8. It appears that from 1947 through 1953 about 10% of

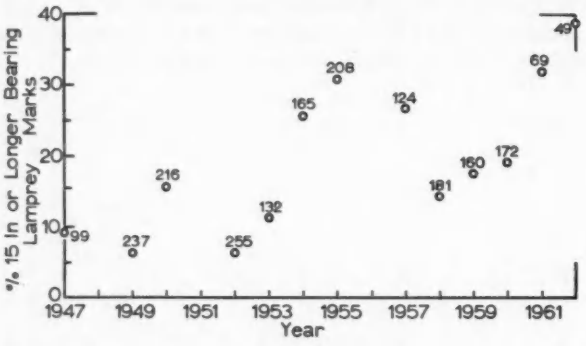

FIG. 8. Percentages of white suckers 15 inches long (38.1 cm) or more in samples of catches in impounding gear in June of various years in South Bay that bore lamprey scars or wounds. Number beside each point represents the sample size.

these fish had been attacked by sea lampreys, and that thereafter there was a definite, if irregular, increase in the incidence of lamprey attacks. The timing of the increased incidence of lamprey attacks coincides with the destruction of the lake trout population. After 1953 the proportion of the larger suckers (15 inches and longer) bearing lamprey scars and wounds increased and the proportion of the larger suckers in samples of catches, and presumably in the population, decreased.

The decline in the proportion of large suckers in catches probably was caused by an actual reduction in numbers of large suckers although it is possible that it was caused by an increase in numbers of small fish. The reduction from the early 1950's to 1964 (Fig. 6B) was from about 60% to about 10%. That decline in proportions of large fish occurring without a reduction in numbers of large suckers would require a six-fold increase in the population of suckers that were less than 15 inches long. It seems likely that such an increase in numbers of fish would have been reflected in the pound net catches even if they were a poor index of population size. It may be concluded, therefore, that there was a decrease in numbers of large fish in the sucker population. The fish grew very slowly, and the other source of recruitment of large fish, immigration, also must have been low, for the decline appears to have occurred when the total annual mortality rate was low, perhaps 25–30%.

The decrease in numbers of large suckers could hardly have been caused by fishing. It was estimated that less than 2% of all sizes of adult suckers

was taken by the fishing gear. It appears that, by far, natural mortality was the greatest source of loss. The decline at low total annual mortality rates indicates, however, that the population of the larger suckers probably could not be sustained under moderate fishing pressure even if fishing mortality were to replace, rather than to act in addition to, natural mortality.

There is no evidence that the white sucker population is smaller now than before the invasion of the sea lamprey. Within 10 years after the collapse of the lake trout population, the pound net catch of suckers was about the same as before 1952 (Fig. 5). If the pound net catch of suckers is a reliable index of the size of the population, it would indicate that after 1957 the sucker population was about the same size as before the invasion of the sea lamprey. However, it is not known if the pound net catch is an accurate indication of the relative size of the sucker population.

Olson (1963) reported that a year after 34% of the estimated white sucker population in Many Point Lake, Minnesota, was removed, there was no reduction in the estimated population. Total annual mortality rates estimated for South Bay suckers were substantially greater than 34% for very large fish, over 18.5 inches, but averaged 25.7% for fish smaller than that, which made up the bulk of the population (probably over 95%) even in the early years. Therefore, if the South Bay population responded in the same manner as the Many Point Lake population, and if the mortality estimates are reasonably accurate, no decline in numbers of suckers in South Bay, except the very large ones, would be expected.

It may be concluded that the sea lamprey has changed the size composition of the white sucker population in South Bay by removing the large fish. It is questionable, however, whether or not it has reduced the size of the sucker population.

ACKNOWLEDGMENTS

The late Mr John C. Budd was director of the South Bay Fisheries Research Station during most of the time that these data were obtained. The staff of the station carried out all of the field work, sampling, and initial recording of data. The information on growth was taken from a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy from the University of Toronto. The manuscript was read by Drs F. E. J. Fry, J. C. MacLeod, E. D. Lane, and Mr W. J. Christie, director of the Glenora Fisheries Station.

REFERENCES

BUDD, J. C. 1956. Movements of tagged whitefish in northern Lake Huron and Georgian Bay. Trans. Am. Fish. Soc., **86**: 128–134.

BUDD, J. C., AND F. E. J. FRY. 1960. Further observations on the survival of yearling lake trout planted in South Bay, Lake Huron. Canadian Fish Culturist, **26**: 7–13.

COBLE, D. W. MS, 1965. On the growth of some Great Lakes fishes with especial reference to temperature. Ph.D. Thesis. University of Toronto, Toronto, Ont.

DENCE, W. A. 1948. Life history, ecology and habits of the dwarf sucker, *Catostomus commersonnii utawana* Mather, at the Huntington Wildlife Station. Roosevelt Wildlife Bull., **8**(4): 81–150.

ESCHMEYER, P. H. 1955. The near extinction of lake trout in Lake Michigan. Trans. Am. Fish. Soc., **85**: 102–119.

FRASER, J. M. 1955. The smallmouth bass fishery of South Bay, Lake Huron. J. Fish. Res. Bd. Canada, **12**(1): 147–177.

FRY, F. E. J. 1952. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc., **82**: 178–192.

FRY, F. E. J., AND J. C. BUDD. 1957. The survival of yearling lake trout planted in South Bay, Lake Huron. Canadian Fish Culturist, **23**: 13–21.

GEEN, G. H., T. G. NORTHCOTE, G. F. HARTMAN, AND C. C. LINDSEY. 1966. Life histories of two species of catostomid fishes in Sixteenmile Lake, British Columbia, with particular reference to inlet stream spawning. J. Fish. Res. Bd. Canada, **23**(11): 1761–1788.

HALL, A. E., JR., AND O. R. ELLIOTT. 1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia, No. 1: 73–74.

HILE, R. 1946. Trends in the lake trout fishery of Lake Huron through 1946. Trans. Am. Fish. Soc., **76**: 121–147.

LAGLER, K. F. 1956. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 421 p.

OLSON, D. E. 1963. Role of the white sucker in Minnesota waters. Proc. Minn. Acad. Sci., **31**(1): 68–73.

OLSON, D. E., AND W. J. SCIDMORE. 1963. Homing tendency of spawning white suckers in Many Point Lake, Minnesota. Trans. Am. Fish. Soc., **92**(1): 13–16.

OVCHYNNYK, M. M. 1965. On age determination with scales and bones of the white sucker, *Catostomus commersoni* (Lacépède). Zool. Anz., **175**: 325–345.

RICKER, W. E. 1937. The concept of confidence or fiducial limits applied to the Poisson frequency distribution. J. Am. Statist. Assoc., **32**: 349–356.

1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada, No. 119. 300 p.

SCOTT, W. B. 1963. A review of the changes in the fish fauna of Ontario. Trans. Roy. Canadian Inst., **34**(2): 111–125.

SNEDECOR, G. W. 1956. Statistical methods. 5th ed. The Iowa State College Press, Ames, Iowa. 534 p.

Distributions of Kraft Mill Effluent in a British Columbia Harbour[1]

By A. E. Werner and W. F. Hyslop

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Concentrations of kraft mill effluent in Alberni Harbour were measured on three occasions: (*a*) after a period during which no effluent had been discharged; (*b*) during the influx of effluent into the almost-clean harbour; and (*c*) after a year of regular effluent discharge. Optical methods were used to measure concentrations. A simple formula was developed to estimate the concentrations of currently or recently discharged effluent. In addition to the mill, another pollution source contributed to the water colour in at least one area. The transient pattern of effluent patches which formed when the mill renewed operations was followed, from the sewer outfall, several miles down the inlet. It resembled the distribution obtained with a hydraulic model of Alberni Harbour developed in the 1940's by another worker. Effluent concentrations after a year of normal operation were recorded; their distribution is discussed.

INTRODUCTION

The temporary shutdown of a kraft pulp and newsprint mill in Port Alberni, B.C., offered an unusual opportunity to study how wastes distribute themselves in comparatively uncontaminated waters.

The flow of effluent from the sewers of the pulp mill of MacMillan, Bloedel and Powell River Ltd. stopped around noon of May 19, 1964. Within 10 days most of the polluted water had disappeared. The outfall from the city's sewer remained the only apparent source of pollution. It gave rise to a faintly brown stream extending some distance out from the shore. Elsewhere the water colour had changed from brown to green, and the transparency had increased considerably.

On July 10, 1964, the mill started to operate again. Soon after, at about 1400 hr (PST), the first effluent issued from the sewer. It was a faintly brown, almost odourless liquid, containing much fibrous material. Eventually a deep-brown effluent appeared and started to spread into the clear waters.

By July 10, 1965, the mill had been operating normally for 12 months, and the water over wide areas had become brown again.

EXPERIMENTAL WORK

Methods

A survey of 12 stations (Fig. 1, A–L) was made on May 28, 1964. The water transparency was measured by Secchi disc. Samples of clear water were

[1]Received for publication February 6, 1967.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

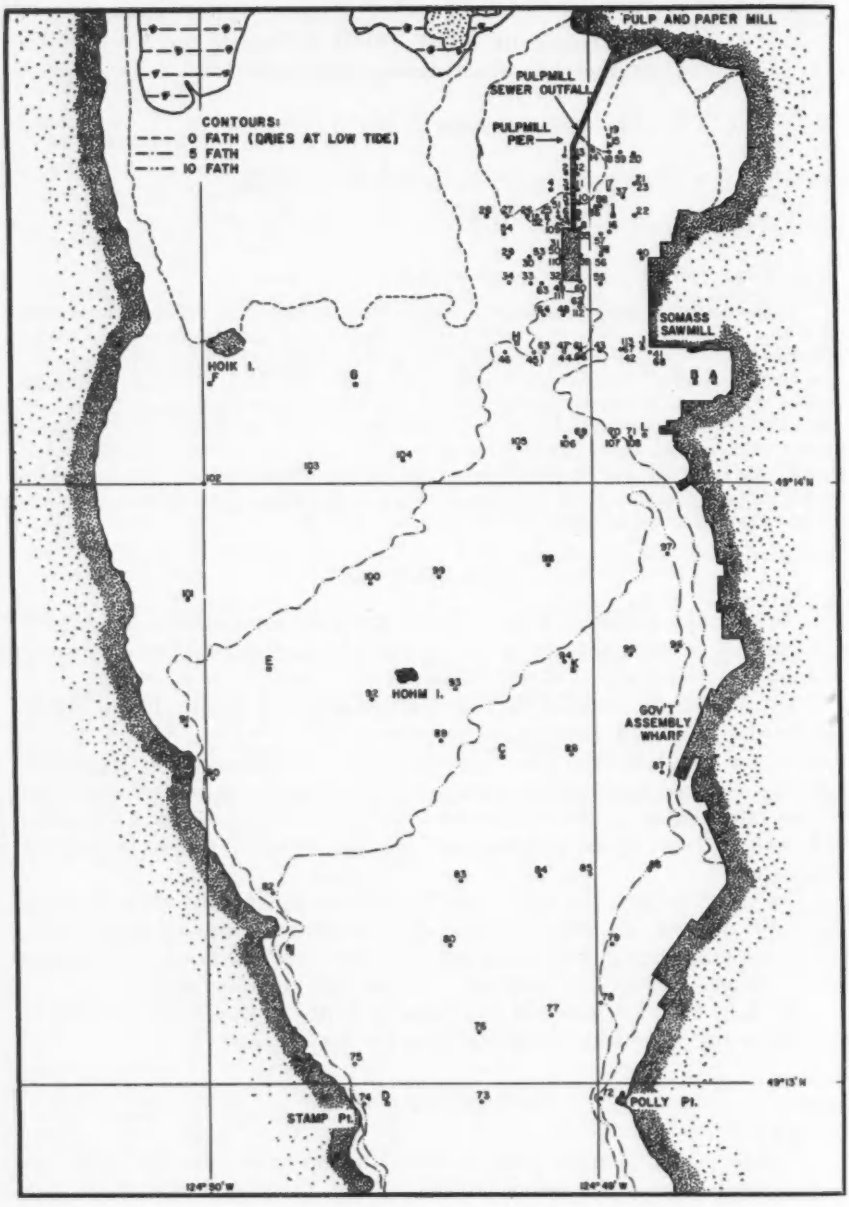

FIG. 1. Stations in Alberni Harbour.

collected at a location near the pulp dock (Station I) and from mid-channel in the vicinity of Hohm Island (Station K).

On July 10 and 11, 1964, a series of stations (Fig. 1, 1–113) was studied from the time the first brown effluent appeared until night fell at around 1930 hr.

The dark-brown effluent was sampled at the flume as soon as it appeared and again a few hours later. Both samples were used to calibrate a Nessler colorimeter in terms of effluent concentration. All surface water samples were tested with this apparatus.

A Secchi disc was lowered at each station to obtain a measure of water transparency. After the 40th station this observation was discontinued because the disc was lost. Further stations were occupied on the following morning from 0848 hr, a new Secchi disc having been obtained. The operations of July 11 terminated around 1200 hr. On both days fine, sunny weather prevailed and there was neither sea nor swell.

A further survey was made on July 12–13, 1965. The same stations were occupied at the same times of day as in the previous year and samples of the mill effluent were drawn for examination of their colour intensity. Good weather favoured the operation again.

Finally, effluent was drawn at 8-hr intervals on July 14 and 15, 1966. During the intervening year the flume had been extended southwest and the outfall was lowered to sea level. This made it difficult to obtain the samples free from dilution.

Apparatus

The Secchi disc used was a standard, 30-cm diam metal plate painted white (Juday and Birge, 1933).

The Nessler apparatus (Fig. 2) had been designed specially for these surveys. It consisted of six tubes (polyvinyl chloride plastic, 38-mm internal diam) of just over 1-m length. These were attached to a turntable so that by rotating, any desired tube could be brought under the eye. The bottom of each tube consisted of a transparent acrylic resin plate (Lucite) which admitted the diffused light reflected by a white circular disk (45-cm diam) situated below. Each tube was filled to a depth of 100 cm with a standard solution. The sample under test was contained in a similar tube which had a hole in the side, exactly 100 cm above the bottom. This ensured a correct sample depth at each filling, any excess draining out. Before visually comparing the optical densities of sample and standards, this hole was closed by a rubber stopper. All samples were filtered through cotton before testing. A few of the samples were too concentrated for direct comparison. They were suitably diluted before comparing them with the standards.

CALCULATIONS

Beer-Lambert's Law was the basis for calculating concentrations:

$$A = ln \frac{I_o}{I} = a \times b \times c \qquad \ldots\ldots(1)$$

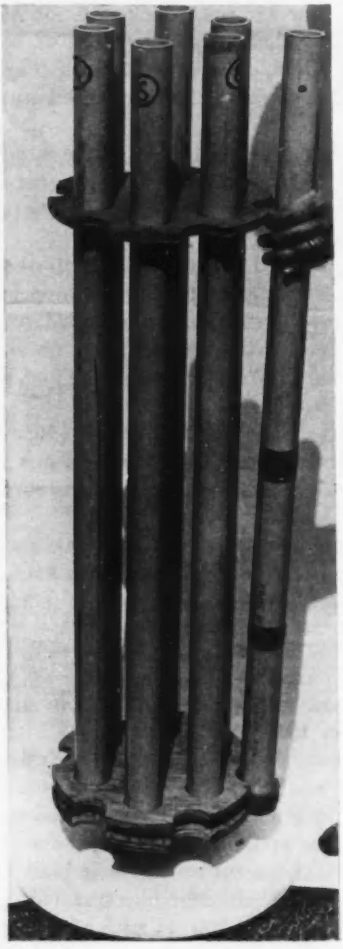

FIG. 2. Nessler apparatus.

A is the absorbance, I_o and I are the light intensities respectively before and after passing through a water column of *b*-metres length and containing colouring matter (kraft mill effluent = K.M.E.) in the concentration *c* (expressed as litres/litre). The absorptivity (per metre), *a*, of the K.M.E. was obtained by the conjoint use of a Nessler tube and a Beckman D.U. spectrophotometer.

In a preliminary Nessler tube experiment, effluent samples were diluted with distilled water until they became just translucent when viewed with the dark-adapted eye through a tube of 1-m length. The average concentrations

at this stage found for the 1964 and 1965 effluents were 122 and 591 ml/litre, respectively. The variations between samples taken on the same day were small in both years (i.e. $\pm 1.65\%$ in 1964 and $\pm 3.85\%$ in 1965); however, the average effluent colour intensity of the later year's samples had decreased markedly from the previous year's average.

The absorbance of a solution of K.M.E. in distilled water, as tested in the spectrophotometer, was a monotonically decreasing function of the wavelength λ in the region of 450–600 mμ (Fig. 3).

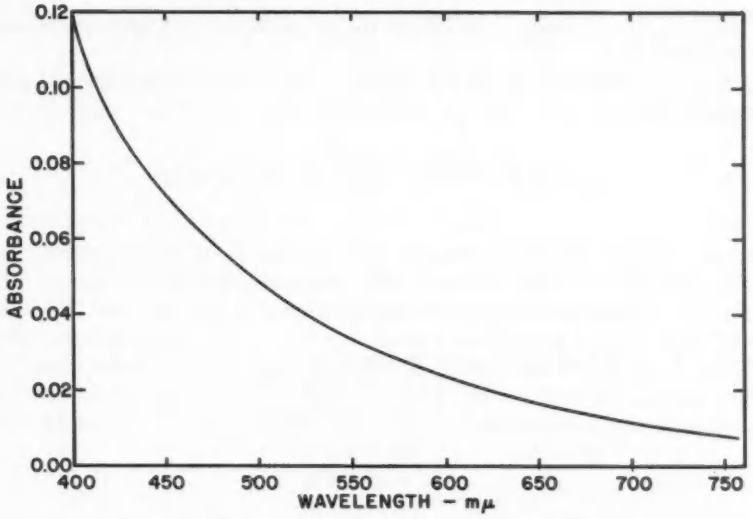

FIG. 3. Absorbance of K.M.E. as function of wavelength.

The absorbance was measured at several concentrations, a curve being prepared for each of several different wavelengths (Fig. 4). From the resulting family of curves the absorbance was read which corresponded to the effluent concentration at the limit of transparency (122 ml/litre) in the Nessler tube. The wavelength chosen was 510 mμ, where the human eye has its maximum sensitivity at low total intensities (Blüh and Elder, 1955; p. 409). Concentrations and cell length (10 cm) were so chosen that the corresponding absorbance readings (A_{10}) fell into the region of the spectrophotometric method's minimum error (Boltz and Schenk, 1963). A value of $A_{10} = 0.2925$ was recorded. The spectrophotometer's absorbance reading, A_{10}, is a function of the transmittance, $T\left(=\frac{I}{I_o}\right)$, namely:

$$A_{10} = \log_{10}\left(\frac{1}{T}\right) = -\log_{10}T \qquad \ldots\ldots(2).$$

The transmitted intensity, I, was calculated as 0.5099 from equation 2, by substituting 0.2925 for A_{10} and unity for incident intensity, I_o. Inserting I together with the cell length l, and the concentration, c, into equation 1 the absorptivity, a, was calculated from the absorbance, A_v, at the vanishing point:

$$A_v = ln\left(\frac{1.0000}{0.5099}\right) = 0.673 = a \times 0.1000 \times 0.122 \quad \ldots\ldots(3)$$

$$a = 55.2; (a' = 11.4).$$

(For convenience a prime was added to all mathematical symbols referring to 1965 effluent.)

The light intensity, I_v, in the Nessler tube at the vanishing point was calculated from:

$$A_v = ln\left(\frac{1.000}{I_v}\right) = 55.2 \times 1.000 \times 0.122 \quad \ldots\ldots(4).$$

This value I_v (= 1/842) can be used to calculate the vanishing depth, D, of a Secchi disc from equation 1. It is only an approximation because in Secchi disc reading the observer's eye is not dark-adapted. Utterback and Jorgensen's (1934) "total vertical absorption coefficient γ" given by Sverdrup et al. (1946, p. 84) as "extinction coefficient (a)" for average coastal water from Juan de Fuca Strait, 0.276, was used. The total light path, b, through water (from the surface to the disc and back to the observer) is twice the measured depth,

$$b = 2D \quad \ldots\ldots(5).$$

The concentration, c, is 1.000 because the water itself is the absorbent. Modified in this way, equation 1 becomes:

$$ln\left(\frac{1}{1/842}\right) = ln842 = 0.276 \times 2D \times 1.000 \quad \ldots\ldots(6).$$

The vanishing depth in coastal water, as calculated by equation 6, was 12.2 m.

This value was used to express the water's natural absorption in terms of C_1, the "equivalent K.M.E. concentration" (= EKMEC). To obtain it in convenient units (ml/litre), the value for c from equation 1 with appropriate substitutions was multiplied by the factor 10^3:

$$C_1 = \frac{6.73 \times 10^3}{2 \times 12.2 \times 55.2} = 5.0 \text{ ml/litre}; (C_1' = 24.2 \text{ ml/litre}).$$

A layer of variable thickness of fresh or brackish water exists near the surface (M. Waldichuk, unpublished results). It is due to runoff, chiefly from

the Somass River. Measurements showed the latter water's light absorption to be comparable to that of Utterback's average coastal seawater.

Even 2 weeks after the mill shut down, light absorption at all stations in the harbour was greater than that for average coastal water. This suggested the persistence of a general background pollution characterized by an EKMEC of C_2. In the most transparent water we encountered, the disc disappeared at 5.8 m, the EKMEC being, by equation 1 again:

$$C_1 + C_2 = \frac{6.73 \times 10^3}{2 \times 5.8 \times 55.2} = 10.5 \text{ ml/litre}; \; (C_1' + C_2' = 50.9 \text{ ml/litre}).$$

If the EKMEC of Utterback's "average coastal seawater," 5.0 ml/litre, is deducted from this value, one obtains the general background pollution:

$$C_2 = 5.5 \text{ ml/litre}; \; (C_2' = 26.7 \text{ ml/litre}).$$

Impurities of local origin (e.g. the city sewer) increased the background level at certain stations. The Secchi disc readings taken during the shutdown period served to determine its magnitude. The corresponding EKMEC values, C_3, of this "area pollution" were calculated from the formula:

$$A_v = 2a \left\{ \underbrace{(C_1 + C_2) \times 10^3 D}_{\substack{\text{coastal seawater} \\ + \text{ general background}}} + \underbrace{C_3 \times 10^3 D}_{\text{area pollution}} \right\} \quad \ldots\ldots(7).$$

Substituting for A_v and $C_1 + C_2$, and solving for C_3, one obtains:

$$C_3 = \frac{6.73 \times 10^{-3}}{55.2 \times D} - 10.5; \; (C_3' = \frac{6.73 \times 10^{-3}}{2 \times 11.4 \times D} - 50.9).$$

A general pollution equation making use of all these parameters was then set up. It permitted calculation of the actual K.M.E. concentration, C_S, present at each station. The values for C_3 were chosen from Table I in accordance with the location of the station under test:

$$A_v = 2a(\underbrace{D \times C_1 \times 10^3}_{\text{coastal seawater}} + \underbrace{D \times C_2 \times 10^3 + D \times C_3 \times 10^3 + D \times C_S \times 10^3}_{\substack{\text{background} \quad \text{area} \quad \text{pulp mill} \\ \text{pollution}}}) \quad \ldots\ldots(8).$$

Now:
$$C_S = \frac{6.73 \times 10^{-3}}{2 \times 55.2 \times D} - (5.0 + 5.5 + C_3).$$

Therefore: $$C_S = \frac{610}{D} - (10.5 + C_3)$$

Similarly: $$C'_S = \frac{295}{D} - (50.9 + C'_3)$$ .....(9).

TABLE I. Area pollution as equivalent K.M.E. concentration C_3.

	C_3 (*ml/litre*)	
Station/year	1964	1965
A	6.2	29.7
B	2.8	13.6
C	2.8	13.6
D*	6.2	29.7
E	2.8	13.6
F	2.8	13.6
G	2.8	13.6
H	0.6	2.9
I	0.6	2.9
J	2.8	13.6
K	2.8	13.6
L	6.2	29.6

*This high value was probably due to recent dumping of dredged material nearby.

In Nessler work, a dilution factor, F, was calculated for samples, which had been diluted before comparison with standards:

$$F = \frac{V_s + V_w}{V_s} \quad .....(10).$$

V_s was the sample volume and V_w the volume of diluent used.

The apparent effluent concentration, C_T, of a diluted seawater sample was considered to consist of the effluent concentration, C_N, and the "equivalent effluent concentration," C_Q, of the water itself plus diluent. C_Q and C'_Q include the EKMEC due to coastal seawater and "area pollution." The general background, C_2, was not found in the surface layer from which the Nessler samples were drawn.

$$C_Q = 5.0 + C_3; \ (C'_Q = 24.2 + C'_3) \quad .....(11).$$

Since C_T equals the K.M.E. concentration of the standard, C_s, the actual effluent concentrations, C_N, of the undiluted seawater samples were calculated by appropriate selection of one of the following formulae:

Year	Stations	Diluent	Formula to use	
1965	1–11	Distilled water	$C_N = C_n \times F - C_Q$	.....(12)
1964	1–113	Coastal seawater	$C_N = F \times (C_n - C_Q)$	.....(13)
1965	12–113	" "		

The standards used in 1965 were made up from 1964 effluent which had lost colour intensity in storage so that now 250 ml/litre were required for extinction in the 1-m tube (as compared to 122 ml/litre in 1964). The concentration in the tubes was accordingly doubled and this resulted in effective (though not actual) standard concentrations, C_n (in ml/litre), approximating those of the previous year (see Table II).

TABLE II. Nessler standard concentrations.

Year	C_n (*ml/litre*)					
1964	0.0	10.0	20.0	30.0	40.0	50.0
1965	0.0	9.8	19.5	29.3	39.0	48.8

When the formulae 12 and 13 were applied to 1965 data, the resulting concentrations were in terms of 1964 K.M.E. To express them in terms of the actual year's effluent, they would have to be multiplied by 4.85, the ratio of the respective absorptivities.

The concentrations finally obtained were grouped for expression as intensities in the pollution field (see Table III).

TABLE III. Classification of pollution intensities

Pollution intensity	ml K.M.E./litre seawater
None	0–10
Light	10–20
Medium	20–100
Heavy	100–1000

The vertical position of the polluted layer was found by comparing the K.M.E. concentrations obtained from the Nessler, C_N, and Secchi disc, C_S, readings. Positive values of the differences

$$\Delta = C_N - C_S \qquad .....(14)$$

indicated pollution of the surface layer, negative values characterized subsurface pollution. Zero differences (including small deviations not exceeding

±10% of the corresponding Cs) suggested that pollution was homogeneous within the depth interval examined.

RESULTS

(*a*) During the period of mill shutdown a general background pollution was found (C_2 = 5.5; C_2' = 26.2 ml/litre). In addition there occurred the polluted regions already mentioned (see Table I).

(*b*) The transient phenomena during the start-up period are summarized in Table IV, where the K.M.E. concentrations which prevailed during the

TABLE IV. Growth of pollution field, July 10–11, 1964.

Sampling times[a] (*hr*)	Stations sampled	Level	Stations in various K.M.E. concentration ranges[b]			
			0–10 ml/litre	10–20	20–100	100–1000
July 10	1–23	Surface	7,16,17, 21–23	4,6,8,9, 19,20	3,5,10–15, 18	1,2
1417–1554		Total	7	6,8,16,17, 19,20,22	3–5,9–15, 18,21,23	1,2
1711–1809	24–46	Surface	28,30,32,33, 36,39–46	31,38	25–27,29 34,35,37	24
		Total	28	30–33,39,40	27,29,34–38	24–26
1811–1912	47–65	Surface	47,48,53, 61,63–65		49,50, 54–56, 58,60,62	51,53,57, 59
		Total		Secchi disc lost at station 41		
1913–1924	66–71	Surface	68–71		66,67	
		Total				
July 11	72–113	Surface	72–108			
0848–1141		Total	72–76,80–93,98–105	77–79,94–97,106,107	109–113	

[a]All times given in Pacific Standard Time (+8 Time Zone).
[b]a = 55.2.

two days of sampling are grouped according to the time elapsed from 1417 hr of July 10, 1964.

At 13 stations the water was sampled two or three times during each survey so that short-term concentration changes could be discovered. Table V shows the initial concentrations followed by those observed after the indicated time intervals had elapsed. The concentrations found by the Nessler method in the surface water and those found in depths explored by Secchi disc are reported.

(*c*) The results of the measurements in 1965 are shown in Table VI. They are grouped similarly to those of 1964, with 1411 hr of July 12, 1965, as "Zero Hour."

(*d*) The absorptivities, a, at 510 mμ of the effluent samples collected in July 1966, are shown in Table VII.

TABLE V. Concentrations of K.M.E. at stations visited repeatedly during each year's survey.

Year	Time interval				Stations	Concentrations (*ml/litre*)					
						In depth ($C_{(S)}$)			In surface ($C_{(N)}$)		
	hr	*min*	*hr*	*min*							
1964	2	25	18	19	6	20	393	67	14	688	89
1965	1	43	18	12		252	106	87	92	95	42
1964	2	26			7	9	190		0	44	
1965	1	44				106	119		112	56	
1964	2	50			8	14	89		14	89	
1965	3	14				138	104		141	42	
1964	0	42	17	20	31	18	N.r.[a]	33	24	59	49
1965	2	21	15	29		42	56	62	24	24	33
1964	0	38	17	23	32	11	N.r.	25	0	39	24
1965	1	02	15	34		46	56	49	14	24	24
1964	0	38			38	22	N.r.		14	29	
1965	0	55				42	37		14	24	
1964	1	13			41	N.r.	N.r.		0	0	
1965	1	29				30	41		14	14	
1964	1	08	16	26	42	N.r.	N.r.	23	0	69	29
1965	1	22	14	40		30	37	39	14	14	24
1964	0	03			44	N.r.	N.r.		0	0	
1965	0	09				27	32		4	4	
1964	0	06			61	N.r.	N.r.		0	34	
1965	0	15				44	40		14	14	
1964	16	31			62	N.r.	56		24	138	
1965	14	53				56	56		24	24	
1964	16	01			70	N.r.	17		4	0	
1965	2	36				40	33		8	8	
1964	16	01			71	N.r.	23		0	0	
1965	2	37				46	33		18	8	

[a]N.r. = No reading.

DISCUSSION

(*a*) The harbour pollution during the period of mill shutdown was comparatively small, and a steady state seemed to prevail. After 2 months, although the K.M.E. had effectively disappeared, the absorbance of the water remained relatively high. This absorbance indicated the presence of a "general background pollution," whereas the "area pollution" more likely consisted of other contributions, such as the domestic wastes of the city.

(*b*) During the start-up period, the vertical distribution of K.M.E. in the immediate vicinity of the mill's sewer outfall was homogeneous. Effluent flowing into the shallow, relatively freshwater of this region dispersed throughout it without becoming stratified. As the pollution expanded into deeper water, the effluent tended to remain in the upper (fresher) layer. Its low initial density, decreased still further by elevated temperature, was responsible for this behaviour.

TABLE VI. Pollution field, July 12–13, 1965.

Sampling times[a] (*hr*)	Stations sampled	Level	Stations in various K.M.E. concentration ranges[b]			
			0–10 ml/litre	10–20	20–100	100–1000
July 12	1–23[c]	Surface		17,18,21–23	6,9,–16,19,20	3,5,7,8,
1411–1609		Total			15–23	3,5–14
1614–1848	24–46	Surface	43,44	27,28,34,36–38,40–42,45	24–26,29–33,35,39,46	
		Total	27		28,30–34,36–46	24–26,29,35
1842–1953	47–65	Surface	47,64	48,55–61,63,65	49–54,62	
		Total			47–51,53–65	52
July 12–13		Surface	70	66–68,71	69	
1955–0741	66–71	Total			66–71	
July 13						
0755–1039	72–113	Surface	73,76,83,88,89,93,99,100,104107,108	72,74,75,78–82,84,86,90–92,94–96,98101–103,105,106	77,85,87,97,109–113	
		Total			72–113	

[a]All times given in Pacific Standard Time (+8 Time Zone).
[b]a = 55.2.
[c]Stations 1, 2, and 4 inaccessible.

TABLE VII. Light absorption of K.M.E. in 1966.

Date	Time (*hr*)	Absorptivity (a_{510})
July 14	0900; 1600	33.4; 32.7
15	0800; 1600	44.9; 22.7

The majority of stations conformed to this distribution, but at a few locations the reverse was true, the effluent concentration being greater in the lower layers. Two mechanisms are suggested for this:

(*1*) Effluent discharging at high tide into seawater of high density and mixing with it creates a brackish, polluted layer. On a falling tide freshwater from the Somass River invades the area forming a layer above the polluted water.

(*2*) At low tide, depressions in the sea floor acquire K.M.E. by direct inflow of heavily polluted water. At the beginning of the following flood,

they become covered with a layer of brackish water. As the tide advances, dense seawater flows beneath the two layers. Thus a polluted layer is wedged between comparatively clean seawater below and slightly polluted brackish water above. K.M.E. from the polluted layer then diffuses into the surrounding area.

The effluent dispersed horizontally, outward from the point of origin (Fig. 5*a–d*). A major stream of polluted water moved southwest until contact

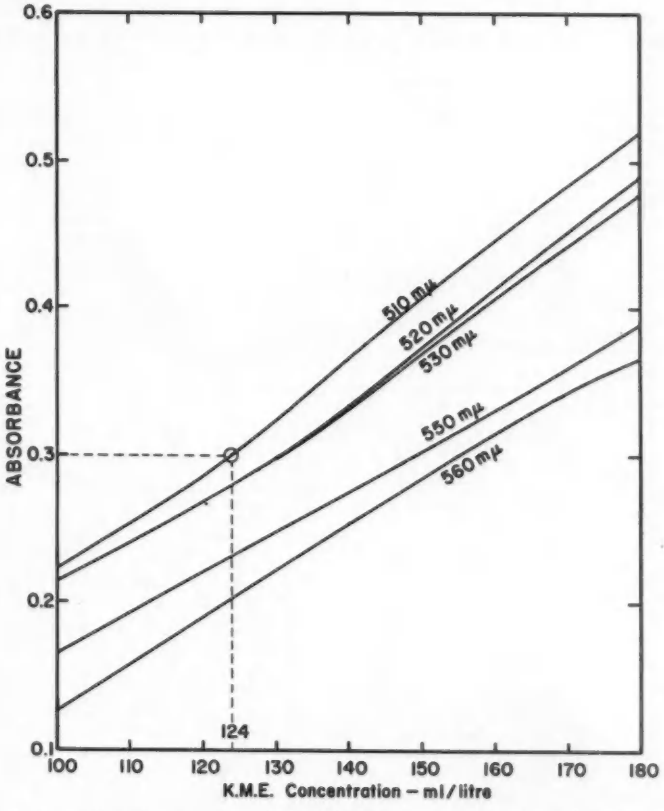

FIG. 4. Absorbance as function of K.M.E. concentration at various wavelengths.

with the Somass River current diverted it southward. A similar but shorter stream moved east. It did so in spite of a falling tide, but within a few hours veered south and became diluted and widely diffused in the inner harbour (Fig. 5*e*). By the following day, three patches of polluted water had moved down the east side of the harbour as far as Polly Point. One of them probably

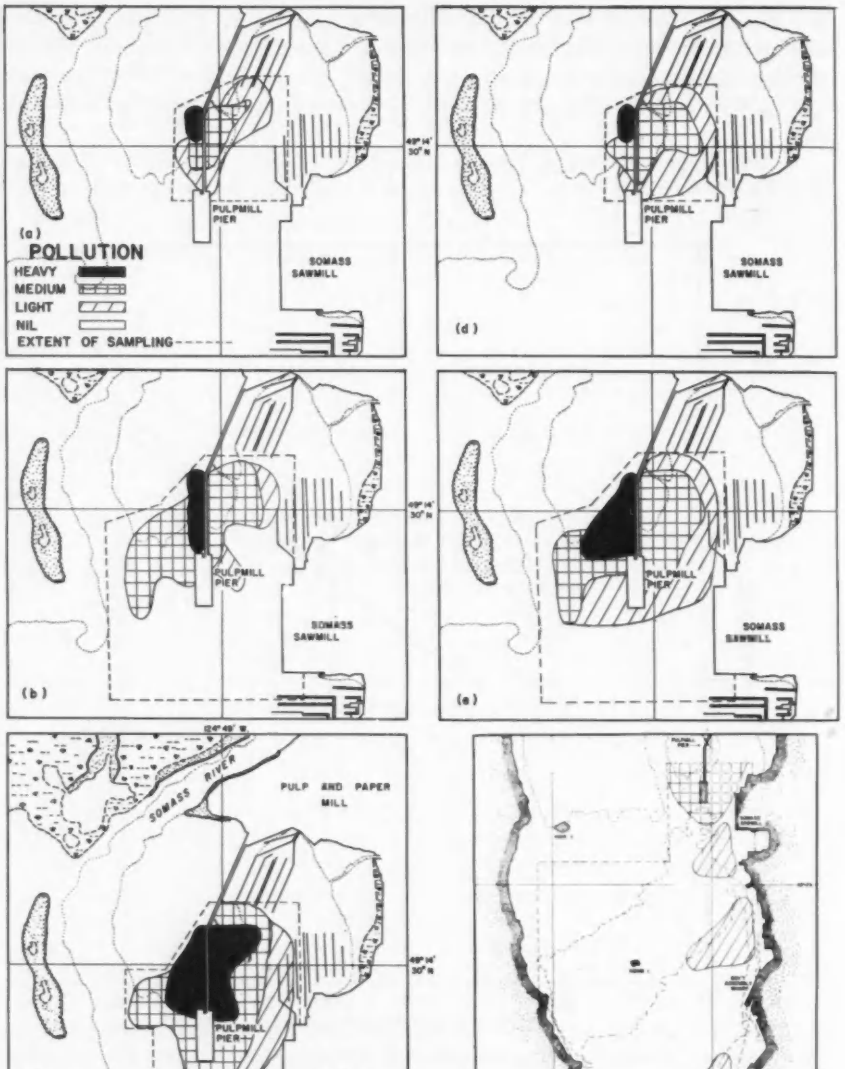

FIG. 5. Pulp mill effluent distributions in Alberni Harbour on July 10 and 11, 1964. (*a*) July 10, from 1411 to 1554 hr (surface); (*b*) July 10, from 1711 to 1809 hr (surface); (*c*) July 10, from 1811 to 1912 hr (surface); (*d*) July 10, from 1417 to 1554 hr (total); (*e*) July 10, from 1711 to 1809 hr (total); (*f*) July 11, from 0848 to 1141 hr (total).

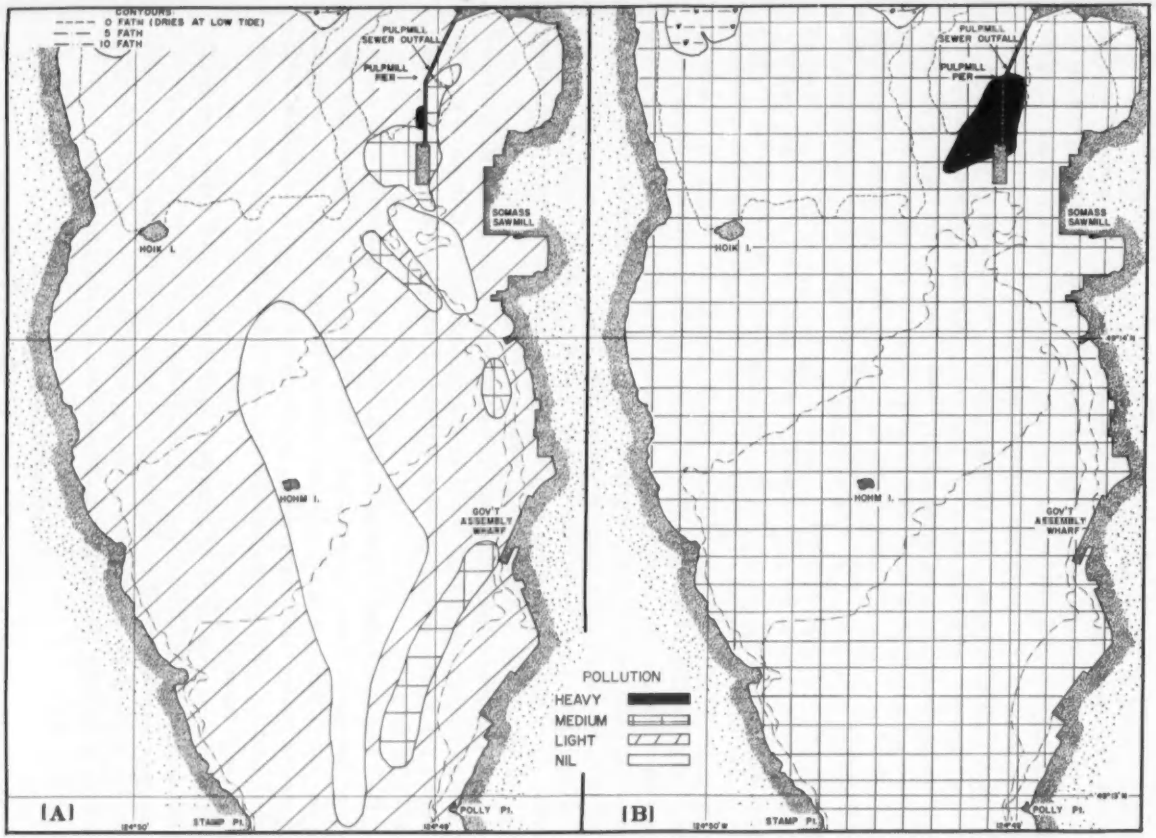

FIG. 6. Pulp mill effluent distribution at the surface (A) and in the layer explored by Secchi disc (B) during July 12–13, 1965.

originated with the city sewer, as it extended in a due westerly direction from the municipal outfall. In spite of the rising tide, no polluted water was found anywhere west of the middle of the harbour (Fig. 5*f*).

The effluent dispersal revealed a pattern very similar to that forecast by Tully (1949) on the basis of his experiments with a hydraulic model of Alberni Inlet. The main differences between predicted and actual distributions were: (i) absence of a predicted patch of high pollutant concentration N and NW of Hohm Island; and (ii) a general trend of the effluent stream to favour the eastern shore more than expected. They may be consequences of the bottom disturbance caused by the tsunami of 1964. Observations after this event showed that gravel beds had been deposited over a region west of the river mouth (between Hohm Island, Hoik Island, and the pulp dock), making it considerably shallower. The wider, and especially the deeper, parts of the harbour appeared less affected.

(*c*) A year after the resumption of mill operations the whole harbour as far as Polly Point was polluted. The lowest effluent concentrations were now found in two patches of superficial river water, one in the centre of the channel, the other southeast of the river mouth. These floated on a body of more heavily polluted water which filled the harbour, with the exception of two structures of very high effluent concentration. The first of these was a plume focussed on the mill's outfall; the second consisted of two discrete elongated patches off the eastern shore (Fig. 6A).

With the exception of the plume, the distributions exhibited by the surface water had no counterpart in the depths explored by Secchi disc where all areas were badly polluted (Fig. 6B).

(*d*) The 1966 effluent obtained from the flume near the outfall, exhibited an average transparency ($\overline{a}_{510} = 33.4$) intermediate between those of the two previous years, the spread between individual samples being much greater (see Table VII).

(*e*) The light absorption of K.M.E. must be interpreted with caution because low lignin concentrations, which are indicated by low light absorption, are not necessarily associated with low effluent toxicity. Many of the effluent's biologically undesirable components (carbohydrates, soaps, sulphides, chlorinated phenols, etc.), are colourless, whereas lignin, though highly coloured, is relatively harmless.

(*f*) The general trend of pollution could be discerned without difficulty in the data presented. However, it is recognized that a fully synoptic picture of the processes described could not be obtained with the facilities available. Also, chemical data were not obtainable; therefore, it was not possible to compare accurately the harbour pollution data of 1964 and 1965.

ACKNOWLEDGMENTS

The authors wish to thank Captain D. Brooks, Harbour Master of Port Alberni, for reporting to them the dramatic clearing of the harbour water after the mill had ceased to operate, thereby revealing the opportunity for

the foregoing study. They are much indebted to Dr M. Waldichuk for offering encouragement and facilities to pursue this problem and providing constructive criticism. Thanks are due to Drs S. Tabata and L. Giovando for reading the manuscript, and also to Messrs A. M. Green, J. H. Meikle, and D. Healey for valuable technical assistance.

REFERENCES

BLÜTH, O., AND J. D. ELDER. 1955. Principles and applications of physics. Oliver and Boyd Publishers, London. 866 p.

BOLTZ, D. F., AND G. H. SCHENK. 1963. Visible and ultraviolet spectrophotometry. *In* L. Meites [ed.] Handbook of analytical chemistry. McGraw-Hill Book Co., New York. Sec. 6. p. 16.

JUDAY, C., AND E. A. BIRGE. 1933. The transparency, the colour and the specific conductance of the lake waters of northeastern Wisconsin. Trans. Wis. Acad. Sci., **28**: 205–259.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING. 1946. The oceans. Prentice-Hall, New York. 1087 p.

TULLY, J. P. 1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. Bull. Fish Res. Bd. Canada, No. 83. 169 p.

UTTERBACK, C. L., AND W. Jorgensen. 1934. Absorption of daylight in the North Pacific Ocean. J. Conseil Conseil Perm. Intern. Exploration Mer, **9**(2): 197–209.

A Preliminary Study of Chromosomes of Two Species of Oysters (*Ostrea lurida* and *Crassostrea gigas*)[1,2]

By Muzammil Ahmed[3] and Albert K. Sparks

College of Fisheries
University of Washington, Seattle, Wash.

ABSTRACT

A diploid chromosome number of 20 ($n = 10$) was found for each of the native oyster *Ostrea lurida*, and the Pacific oyster *Crassostrea gigas*. The diploid complements of the native oyster were normal but in the Pacific oyster atypical numbers, polyploid nuclei, and abnormal cleavage was observed in some somatic metaphase plates. The diplotene meiotic bivalents of the native oyster resembled lampbrush chromosomes.

INTRODUCTION

The objective of this paper is to report the number and gross morphology of chromosomes of the native oyster *Ostrea lurida*, and the Pacific oyster *Crassostrea gigas*, in view of great lack of information on chromosomes of commercial bivalves. Few reports have been published on chromosomes of bivalves and in only one or two cases was a direct investigation of the numbers and gross morphology of chromosomes undertaken. Coe (1931, 1932) could not determine accurately the chromosome number of the two species *Ostrea lurida* and *Crassostrea virginica* but figured 10 chromosome pairs for the former species. Inaba (1936) showed the haploid chromosome number of *Crassostrea gigas* as 9 and Cleland (1947) believed 10 to be the most common diploid number for the Sydney rock oyster, *Crassostrea commercialis*. Recently, Rosenfield (1963) tentatively assigned a diploid chromosome number of 10 to *C. virginica*, *C. gigas*, *O. lurida*, and *O. edulis*. Menzel and Menzel (1965) published a haploid number of 19 ($2n = 38$) for the quahog clams, *Mercenaria mercenaria*, *M. campechiensis*, and their hybrids and discussed the gross morphology of chromosomes.

In the case of oysters, reports on chromosome counts have been only too confusing and the present work is an attempt to further our understanding of their chromosome cytology before genetic and racial investigation could be started.

MATERIAL AND METHODS

The experimental oysters were collected during the summer months of 1966 from Oyster Bay, Willapa Bay, and Hood Canal in the State of Washing-

[1]Received for publication May 1, 1967.
[2]Contribution No. 262 from the College of Fisheries, University of Washington, Seattle, Wash.
[3]Permanent address: Department of Zoology, University of Karachi, Karachi, Pakistan.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

ton, and from Humboldt Bay in California. For studies of *O. lurida* chromosomes, early cleavage embryos were obtained from "white-sick" oysters. No uncleaved eggs could be recovered, and meiotic chromosomes were studied in primary oocytes obtained by stripping ripe but unspent female gonads. The *C. gigas* oocytes were also obtained by stripping mature gonads and fertilized in vitro by adding effective sperm suspension. Samples of oocytes were fixed immediately after adding sperm and then at 10-min intervals up to 2 hr. Samples of unfertilized oocytes were also fixed and preserved.

All samples were fixed and preserved in Carnoy's fluid (1 part glacial acetic acid and 3 parts absolute ethyl alcohol). Squash preparations of the oocytes and embryos were made following the method described by Darlington and La Cour (1962). Iron aceto-carmine and aceto-orcein were used interchangeably for staining purposes. For routine cytological examinations and photomicrography, a Zeiss photomicroscope was used. A green filter was regularly used during bright-field as well as phase-contrast photography. Chromosome counts were made from more than a hundred oocyte nuclei of each of the two species of oysters.

OSTREA LURIDA CHROMOSOMES

In all primary oocyte nuclei examined, a consistent count of 10 meiotic bivalents was made. In different lots of oocytes the meiotic bivalents were generally seen at diplotene or diakinesis, perhaps depending on the state of maturation of the oocytes. The diplotene bivalents were large and resembled in appearance the diplotene lampbrush chromosomes reported by Callan (1957) from the yolk-rich oocytes of the cephalopod *Sepia officinalis*, the isopod crustacean *Anilocra physodes*, an elasmobranch, and amphibians. The lateral loops arising out of the chromosome axis were comparatively small because there is not as much yolk. Two diplotene bivalents of *O. lurida* are shown (Fig. 1*a* and *b*). The diakinesis bivalents (Fig. 2) were homomorphic, irregular in structure, and difficult to characterize with reference to centromere position. Associated with diplotene and diakinesis bivalents were spherical vacuolated bodies that resembled nucleoli (Fig. 1*b*). Metaphase 1 bivalents could not be studied since no uncleaved eggs were found in the mantle cavities of the oysters.

In many 3rd and 4th cleavage embryos, nuclei were seen at resting stages. In such cases, discrete, lightly stained vacuolated spherical bodies were interspersed within the chromatin network (Fig. 3). In well-defined and suitably flattened nuclei, as many as 20 of these spherical bodies of different sizes could be counted. A single well-defined nucleolus was never seen in any of the meiotic and mitotic nuclei and it is thought that these spherical bodies may be nucleoli.

Mitotic chromosomes were studied in lateral as well as polar views (Fig. 4–6), with well-spread metaphase plates available in many of the preparations. Such chromosomes were densely stained and their chromatids could often be seen. Of the 20 chromosomes counted with certainty ($2n = 20$), seven pairs

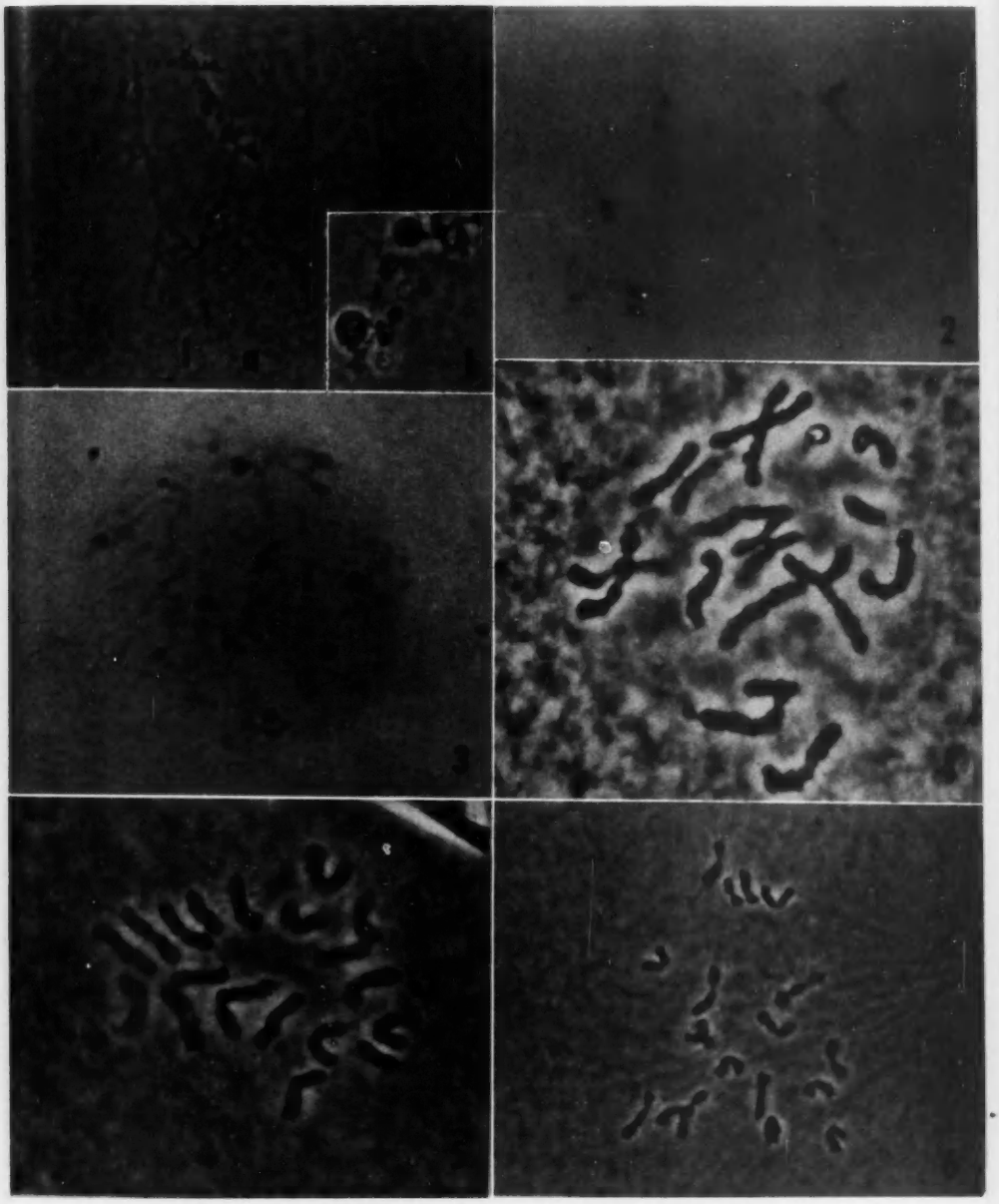

FIG. 1–6. Chromosomes of *Ostrea lurida*. Figures 2 and 3 with bright field illumination; rest with phase contrast.

FIG. 1. Two bivalents of the lampbrush type. One in the inset (*b*) shows associated "nucleoli." 1200×.

FIG. 2. Ten diakinesis bivalents. 480×.

FIG. 3. "Nucleoli" interspersed in chromatin network in a mitotic interphase nucleus. 1920×.

FIG. 4. Twenty late prophase chromosomes from a 3rd cleavage nucleus. SAT-chromosomes can be seen. One chromosome slightly out of focus. 1920×.

FIG. 5. Twenty metaphase chromosomes in polar view. Centromeres are clearly seen. 1920×.

FIG. 6. Twenty metaphase chromosomes in lateral view. Centromeres and chromatids are seen. 1200×.

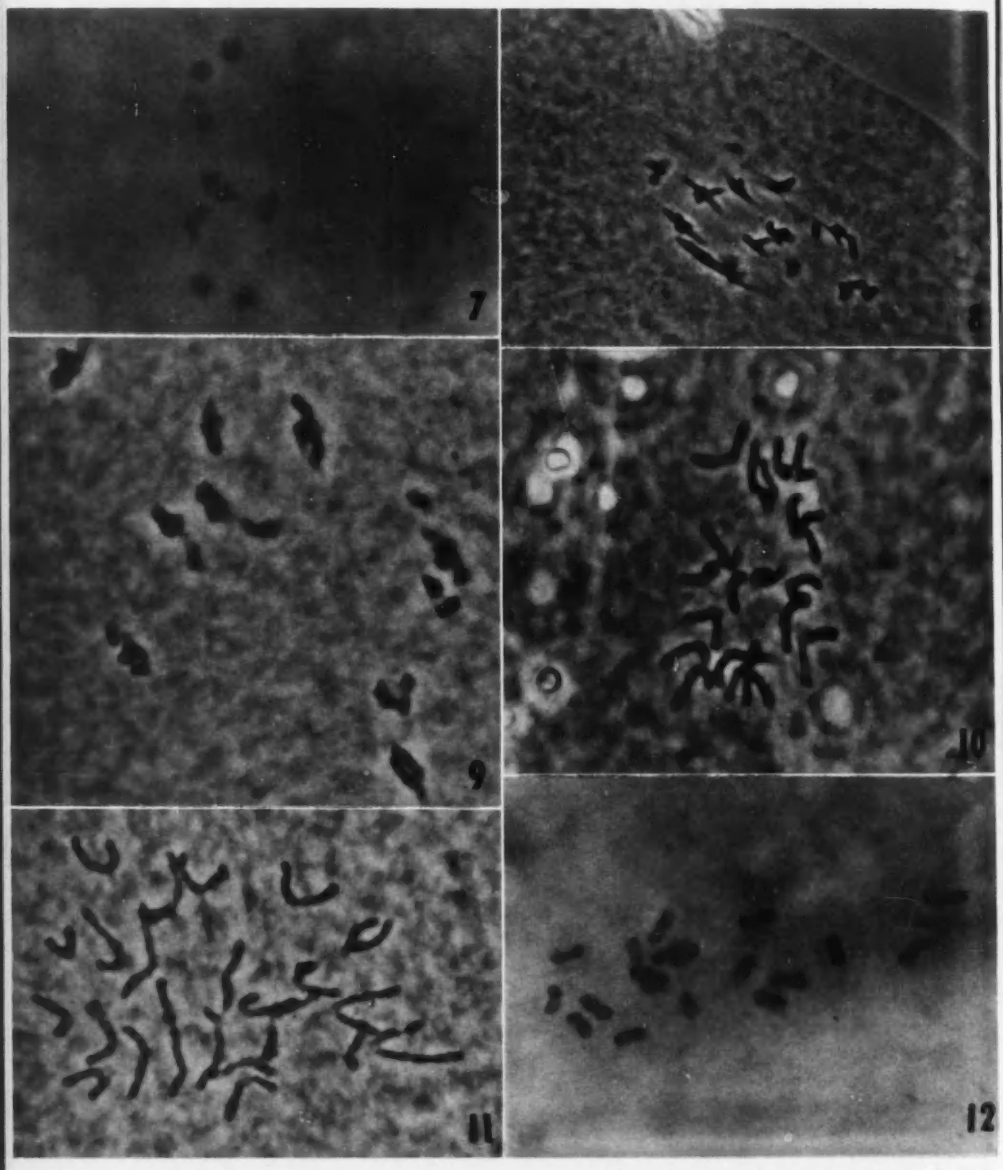

FIG. 7–12. Chromosomes of *Crassostrea gigas*. Figures 7 and 12 with bright field illumination; rest with phase contrast.

FIG. 7. Ten highly condensed metaphase-1 bivalents 30 min after sperm addition. 1920×.

FIG. 8. Ten metaphase-1 bivalents in uncleaved eggs fixed at 2 hr after sperm addition. 1200×.

FIG. 9. Ten metaphase-1 bivalents fixed at 2 hr after sperm addition. 1920×.

FIG. 10. Twenty metaphase chromosomes from a 2nd cleavage nucleus. 1920×.

FIG. 11. Somatic metaphase plate showing atypical chromosome number. 23 chromosomes. Satellite bodies can be seen. 1920×.

FIG. 12. Twenty highly condensed mitotic metaphase chromosomes. 1920×.

were metacentric or approximately so and three pairs submetacentric. This is however, a tentative grouping and karyotype analysis should be made. Although no SAT-chromosomes (bearing satellite bodies) were seen at late metaphase, at least one pair was seen with satellites in late prophase (Fig. 4). Late metaphase chromosomes of 3rd cleavage nuclei range from 1.2 μ to 5 μ in length and chromosomes in later cleavage nuclei are considerably smaller. Sex chromosomes could not be distinguished.

CRASSOSTREA GIGAS CHROMOSOMES

In primary oocyte nuclei, the meiotic bivalents were seen at diplotene, were large and fuzzy, and stained lightly. No lateral loops were observed on the chromosome axis. They were scattered along the nuclear membrane, with one or two present near a large nucleolus within the spacious nuclear cavity. The bivalents were seen to pass through progressive condensation in oocytes fixed at 10–60 min after addition of sperm. The first maturation spindle could be seen within 60 min after fertilization and up to 15 hr or more in uncleaved eggs.

In oocytes fixed at 10–60 min after sperm addition, meiotic bivalents were seen at metaphase 1 and were highly condensed and homomorphic (Fig. 7). In oocytes where no development had taken place even after 15 hr with sperm addition the metaphase-1 bivalents were considerably larger (Fig. 8 and 9). Ten bivalents were usually observed in suitable preparations.

In the nuclei of 2–8 cell embryos, polar and lateral views of diploid metaphase plates were examined for chromosome counts (Fig. 10–12). Twenty chromosomes were usually present ($2n = 20$) but atypical numbers were observed in some plates (Fig. 11). The chromosomes were densely stained and their centromeres and individual chromatids could often be observed. When compared with metaphase chromosomes of *O. lurida*, they were generally more slender and less strongly coiled. In 3rd cleavage nuclei they measured approximately 1.8 μ–6 μ. They can be tentatively grouped as 8 metacentric or approximately metacentric pairs and 2 submetacentric pairs. As in *O. lurida* no heteromorphic sex chromosomes were found.

A high degree of abnormality in cleavage of many eggs, associated with monoploid, triploid, and tetraploid complements, was observed. In few nuclei, extreme fragmentation of chromatin material was evident and in others the chromosomes were too numerous to be counted. Many cells failed to undergo cleavage and the cytology of the maturation divisions of others resembled the development of *C. gigas* in which artificial parthenogenesis was induced by Inaba (1936).

DISCUSSION

This study of meiotic and mitotic chromosomes indicates that both species of oysters possess a diploid chromosome number of 20 ($n = 10$). Coe (1931) studied spermatogenesis in *O. lurida* and noted that the chromosome number was not large, but he could not determine the number with certainty

because of the crowded condition of the metaphase and anaphase plates. However, in semidiagramatic drawings, 10 chromosome pairs were shown. Similarly, in studying spermatogenesis of the American oyster, *C. virginica*, the chromosome number could not be determined with accuracy (Coe, 1932). Perhaps the most useful account published on the number and behavior of chromosomes in an oyster species is that of Inaba (1936) in which he described in fair detail the behavior of chromosomes in normal and abnormal meioses and mitoses in *C. gigas* eggs. Although his major concern was the cytology of artificially induced parthenogenesis, study of fertilized eggs indicated that the haploid chromosome number was 9. In *C. commercialis*, Cleland (1947) counted a maximum of 5 meiotic bivalents and 8–11 mitotic chromosomes but he indicated that 10 was the most common number at 2–4 cell stage in fertilized eggs. The studies published by the three workers, Coe (1931), Inaba (1936), and Cleland (1947) were based on cytological examination of stained sections of paraffin-embedded gonads or eggs.

Rosenfield's (1963) tentative counts of $2n = 10$ for each of *C. virginica*, *C. gigas*, *O. lurida*, and *O. edulis* (with some question that the diploid number for *C. virginica* may be either 8 or 10) do not agree with our counts of $2n = 20$ ($n = 10$) for *O. lurida* and *C. gigas*.

In our cytological investigations the diploid complements of *O. lurida* were regular in number but in the case of *C. gigas* few atypical counts were made and fragmentation of chromosomes and polyploid nuclei were seen. Polyploid nuclei were also reported in hybrid F_2 embryos of the quahog clams, *M. mercenaria* and *M. campechiensis* (Menzel and Menzel, 1965). Perhaps polyspermy, endomitosis, or some degree of parthenogenetic development, besides other causes, might have induced abnormalities.

In both species of oysters investigated, the primary oocyte nuclei were seen at diplotene or diakinesis and not metaphase 1 as shown by Menzel and Menzel (1965) for the quahog clams and their hybrids and as our own studies have shown for the butterclams *Saxidomus giganteus* and *S. nuttalli* and the mussels *Mytilus californianus* and *M. edulis* (unpublished results). After the sperm penetrates the egg, the following events set in: diplotene-diakinesis bivalents condense in an attempt to reach metaphase 1; maturation divisions occur; polar bodies are extruded; formation of zygote follows by the fusion of male and female pronuclei; and cleavage occurs.

Although the two species of oysters have the same chromosome number, the shape, size, and the coiling behavior of the chromosomes at identical stages of development is different in both meiotic and mitotic chromosomes. The diplotene bivalents in the maturing oocytes of *O. lurida* are of the lampbrush type whereas those of *C. gigas*, although fuzzy in appearance, do not "spin out" similar loops. This may be related to the fact that the oocytes of *O. lurida* contain comparatively more yolk and are about twice as large as those of *C. gigas*. It must be remembered here that *O. lurida* is a larviparous species and the activity of the lampbrush bivalents in oocytes is connected with the production of enough yolk for the developing embryos.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to Dr Herschel L. Roman, Chairman, Department of Genetics, and Dr W. Siang Hsu, Department of Zoology, University of Washington, for their comments, suggestions, and critical evaluation of the manuscript; and to Dr Kenneth K. Chew and Mr Donald Weitkamp of the College of Fisheries, University of Washington, for their help in the procurement of experimental oysters.

REFERENCES

CALLAN, H. G. 1957. The lampbrush chromosomes of *Sepia officinalis* L., *Anilocra physodes* L. and *Scyllium catulus* Cuv. and their structural relationship to the lampbrush chromosomes of amphibia. Publ. Staz., Zool. Napoli, **29**: 329–346.

CLELAND, K. W. 1947. Some observations on the cytology of oogenesis in the Sydney rock oyster (*Ostrea commercialis* I. and R.). Proc. Linnean, Soc. N.S. Wales, **72**: 159–182.

COE, W. R. 1931. Spermatogenesis in the California oyster (*Ostrea lurida*). Biol. Bull., **61**(3): 309–315.

1932. Sexual phases in American oyster (*Ostrea virginica*). Ibid., **63**(3): 419–444.

DARLINGTON, C. D., AND L. F. LA COUR. 1962. The handling of chromosomes. Hafner Publishing Company, New York. 263 p.

INABA, F. 1936. Studies on the artificial parthenogenesis of *Ostrea gigas* Thunberg. J. Sci. Hiroshima Univ., Ser. B1, **5**: 29–46.

MENZEL, R. W., AND M. Y. MENZEL. 1965. Chromosomes of two species of quahog clams and their hybrids. Biol. Bull., **129**(1): 181–188.

ROSENFIELD, A. 1963. Some cytological and chemical characteristics of the Ostreidae. Nat. Shellfish. Assoc., Abstracts of Formal Papers.

Ecological Specificity of Parasites of Some Embiotocid Fishes[1,2]

By Hisao P. Arai

Department of Biology
University of Calgary, Calgary, Alta.

ABSTRACT

An investigation of the relative roles of phylogenetic and ecological factors in determining host specificity at the intrafamilial level in fishes of the family Embiotocidae has been made. The results do not show indications that specificity is related to host phylogeny, i.e. parallel host–parasite evolution is not apparent. However, data are presented which strongly support the contention that specificity of parasites in *Cymatogaster aggregata* is determined by factors which are of an ecological nature.

INTRODUCTION

One of the more interesting questions in parasitology is that of host specificity, i.e. the adaptation and restriction of parasites to one particular taxon of hosts. The application of knowledge of this specificity to the solution of problems on the phylogeny and past distribution of hosts was first published by von Ihering (1891). Metcalf (1929), who made extensive use of parasitological data in proposing relationships and paths of dispersal of amphibians, termed this approach to the study of phylogenetic and zoogeographic questions, the "Von Ihering method." Subsequent workers have applied the "Von Ihering method," in varying degrees, to a number of host–parasite groups. For example, Baer (1947), Dougherty (1949), and Gambino and Heyneman (1960) have utilized this method for the cestodes of birds, the nematodes of mammals, and the nematodes of lizards, respectively. Manter (1957) has made a comprehensive study of host specificity in the digenetic trematodes of fishes. In addition, a series of other reports discussing host specificity data as aids in solving problems of host phylogeny was presented under the editorship of Baer (1957). The supporting evidence given for the thesis that parallel host–parasite evolution has occurred was generally obtained from recoveries of related parasites from related hosts. The extent of parallel evolution shown from these examples ranged from a single species of parasite limited in its distribution to two sibling species of hosts to related families of parasites found in hosts referable to taxa at or above the ordinal level. In many cases where studies of this nature have been made, the various authors have concluded or strongly implied that the phylogeny of the respective parasite does parallel the evolutionary lines of the host groups.

[1]Received for publication July 7, 1967.
[2]This work was initiated at the Department of Zoology, University of California, Los Angeles and completed at the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

Other workers (e.g. Baylis, 1938; Baer, 1951; Noble, 1941, 1957) have warned that the "Von Ihering" method must be used with caution and that ecological factors may be as or more important than phylogenetic ones in determining the parasite fauna of a given taxon of animals. V. A. Dogiel and various members of his school of parasitologists in the USSR stand out as strong proponents of this view. Dogiel (1962) has summarized his opinions in his book, *General Parasitology*. The results of the studies which Dogiel presented indicate that a variety of factors can determine or influence the parasite fauna of any species or group of hosts. The authors to which Dogiel has referred have shown that, among others, the age of the host, season of the year, food of the host, host's mode of life, and geographical distribution of the hosts do modify or alter the helminth fauna of a host population with reference to time and space.

The present work was initiated to determine the feasibility of utilizing digenetic trematodes as indicators of intrafamilial phylogeny in the marine fish family, Embiotocidae. The preliminary results of the study indicated that factors other than phylogenetic proximity of the hosts were determining the extent and degree of parasitism. As a result, two aspects of the ecology of the hosts were taken into consideration, i.e. the habitat of the host and the geographical distribution of the host in evaluating their respective roles in the pattern of parasitism which exists in the embiotocid fishes.

MATERIALS AND METHODS

In the earlier portions of this study, embiotocid hosts were collected along with other fishes as a part of a general survey of helminth parasites of marine fishes of the Californias. For purposes of this present report, only 15 species of host fishes have been considered. These fishes were collected with the use of poisons, seines, spear-fishing guns, trawls, and traps. The California collections were made whenever an opportunity was available. However, to minimize differences which could occur as a result of seasonal changes in the helminth fauna, subsequent collections in British Columbia were made as simultaneously as possible.

Examinations of the fishes for parasites were made either immediately after collection or over a period of time on frozen specimens. These examinations were made with the aid of a stereoscopic microscope using magnifications of 20× through 60×. Helminths were heat- or cold-killed and preserved in either an alcohol–formalin–acetic acid mixture or in 70% ethanol. Flatworms and acanthocephalans were stained in a conventional manner with either Semichon's acetocarmine or with hematoxylin (Kornhauser's or Delafield's modifications). Nematodes and copepods were studied as wet mounts when cleared with lactophenol and a mixture of ethanol and glycerine, respectively.

RESULTS

For the California populations of embiotocids, analysis of the host range of parasitic species was limited to digenetic trematodes. Cestodes, nematodes,

and acanthocephalans were represented by larval stages only. Since specific identification of these latter forms was not possible, they were not included in the analysis of host relationships. Host distribution of the trematodes is shown in Table I.

TABLE I. Numbers of embiotocid fishes infected with digenetic trematodes. Numbers in parentheses after each host name indicate number of each species examined.

Hosts	Parasites[a]													
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Amphigonopterus aurora (3)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphistichus argenteus (26)	–	–	5	2	–	–	–	–	15	2	–	–	–	2
Brachyistеus aletes (3)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
B. frenatus (2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cymatogaster aggregata (59)	–	–	2	–	–	–	–	–	–	–	–	–	–	1
Embiotoca jacksoni (167)	1	–	–	–	2	–	1	–	–	–	53	83	–	–
E. lateralis (16)	–	–	–	–	–	–	–	–	–	–	9	5	–	–
Hyperprosopon anale (5)	–	–	1	–	–	–	–	–	–	–	2	–	–	–
H. argenteum (96)	–	–	2	–	–	1	–	2	1	–	–	–	–	–
Hypsurus caryi (2)	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Micrometrus minimus (107)	–	–	1	–	–	–	–	1	–	–	–	2	–	–
Phanerodon furcatus (59)	–	–	3	–	1	–	2	–	–	–	5	4	–	–
Rhacochilus toxotes (9)	–	–	–	–	–	–	–	–	–	–	1	3	–	–
R. vacca (28)	–	–	–	–	–	–	2	–	–	–	2	4	–	–
Zalembius rosaceus (20)	–	12	–	–	–	–	–	–	–	–	–	4	–	–

[a]Parasites: A = *Stephanostomum dentatum*; B = *Labrifer* sp.; C = *Genitocotyle acirrus*; D = *Diplangus triradiatus*; E = *D. paxillus*; F = *Neochasmus* sp.; G = *Proctoeces macrovitellosus*; H = *Schikhobalotrema girellae*; I = *Lasiotocus* sp.; J = *Monorchis* sp.; K = *Telolecithus pugetensis*; L = *Neozoogonus californicus*; M = *Helicometrina nimia*; N = *Pseudopecoelus umbrinae*.

It is clear from these results that some of the trematodes show little in the way of strict species specificity. *Genitocotyle acirrus* (C), *Telolecithus pugetensis* (K), and *Neozoogonus californicus* (L) are examples of this lack of species specificity. Although at least two species, *Labrifer* sp. (B) and *Lasiotocus* sp. (I), do exhibit a tendency to be host specific, the nature of the specificity (phylogenetic or ecological) requires further examination. However, because of inadequate sample sizes for some host species and the low incidence of infection by most trematodes, further evaluation of these data cannot be considered.

Considering all data presented in Table I, a pattern of specificity reflecting intrafamilial host phylogeny is not apparent.

In Tables II, III, and IV data on occurrence of the three most common species is presented according to habitats in which the hosts were collected. The habitats numbered 1–5 are: (1) the rocky lower intertidal and subtidal zones; (2) the intertidal and subtidal zones along a mixed sand–rock shore; (3) the sandy intertidal and subtidal zones; (4) the estuarine *Zostera marina* community; and (5) the estuarine mud-bottom habitat.

In Table II it is clear that the main habitat from which fishes infected with *T. pugetensis* were taken was an estuarine eelgrass (*Z. marina*) community. The exception of the three specimens of *E. jacksoni* from Habitat 1

TABLE II. Ratio of number of fish infected with *Telolecithus pugetensis* to number of fish examined in four different habitats. Numbers in parentheses after each of the host names indicate the total number of each species examined.

Host species	Habitats[a]			
	1	2	3	4
Embiotoca jacksoni (167)	3/4	0/1	0/3	50/159
E. lateralis (16)	0/1	0/0	0/0	9/15
Rhacochilus toxotes (9)	0/0	0/0	0/0	1/9
R. vacca (28)	0/0	0/0	0/6	2/22
Phanerodon furcatus (59)	0/0	0/0	0/7	5/52
Hyperprosopon anale (5)	0/0	0/0	0/0	2/5

[a]1, the rocky lower intertidal and subtidal zones; 2, the intertidal and subtidal zones along a mixed sand–rock shore; 3, the sandy intertidal and subtidal zones; 4, the estuarine *Zostera marina* community.

should be clarified in that these fish were also collected from an eelgrass bed. In this case, however, the eelgrass was located in relatively deep water and offshore from a rocky beach. The specimen of *E. lateralis* (habitat 1) was taken in the same collection as the three *E. jacksoni* mentioned above.

In Table III the primary habitat from which fishes infected with *N. californicus* were collected is again the estuarine *Zostera* beds. All fishes examined from habitats 1 (*E. jacksoni* and *E. lateralis*) and 2 (*E. jacksoni*, *E.*

TABLE III. Ratio of number of fish infected with *Neozoogonus californicus* to number of fish examined in four different habitats.

Host species	Habitats[a]			
	1	2	3	4
Embiotoca jacksoni (167)	3/4	1/1	0/3	84/159
E. lateralis (16)	0/1	0/0	0/0	5/15
Micrometrus minimus (107)	0/0	0/0	0/27	2/80
Phanerodon furcarus (59)	0/0	0/0	0/7	4/52
Rhacochilus toxotes (9)	0/0	0/0	0/0	3/9
R. vacca (28)	0/0	0/0	0/6	4/22
Zalembius rosaceus (20)	0/0	4/20	0/0	0/0
Hypsurus caryi (2)	0/0	1/1	0/1	0/0

[a]See footnote a, Table II.

lateralis, *Z. rosaceus*, and *H. caryi*) are from deepwater *Zostera* environments, one being offshore from a rocky beach and the other from a rock–sand tidal zone.

In Table IV even where larger samples of one host were collected from two or more habitats no definite correlation between parasitism and habitat can be observed.

TABLE IV. Ratio of number of fish infected with *Genitocotyle acirrus* to number of fish examined in five different habitats.

Host species	Habitats[a]				
	1	2	3	4	5[b]
Amphistichus argenteus (26)	0/0	0/2	5/24	0/0	0/0
Cymatogaster aggregata (59)	0/0	0/1	2/45	0/1	0/12
Hyperprosopon anale (5)	0/0	0/0	0/0	1/5	0/0
H. argenteum (96)	0/0	0/13	2/53	0/30	0/0
Micrometrus minimus (107)	0/0	0/0	0/27	1/80	0/0

[a]For description of habitats 1–4, see footnote a, Table II.
[b]5, the estuarine mud-bottom habitat.

Although chi-square analyses ($p = 0.10$) do not show significant differences in the incidences of infection for any host species taken in two or more habitats, the data presented in Tables II–IV suggest that ecological, rather than phylogenetic, factors are operating in determining the parasite fauna of a given species of host; that is, some of the Digenea show a restriction to only one or two types of environments. However, the chronology of host collections and, as emphasized above, the small sample sizes of host collections from some of the habitats prevent further evaluation or conclusions to be drawn from these results.

As previously indicated, the data presented in Tables II–IV were collected over a period of time, i.e. with little regard to the possibility of differences in the parasite faunas resulting from seasonal changes. To eliminate this possible source of variability, a series of collections of one host species, *Cymatogaster aggregata*, was made. Two of the collections were made, 6 days apart, in 1963 at Departure Bay on Vancouver Island and at Bowen Island in Howe Sound, British Columbia. These localities are some 40 miles apart and separated by the Strait of Georgia. The Departure Bay collection site was represented by a small *Zostera* bed located on a relatively flat, sand–rock beach; the Bowen Island site was at the base of a sheer rock cliff, extending down into the sea along a talus slope which was sparsely covered with a variety of marine algae. The depth of capture of the fish was to approximately 60 ft. Another two collections, separated by 4 days, were made in 1964 at Croyden Bay and Elcho Harbour, also in British Columbia. The distance

between these localities is some 50 miles. The latter locality was a *Zostera* community located on the delta of a small stream emptying into the head of a short inlet. The former site was in a small bay formed by high rocky cliffs which extend into the water to depths of over 100 fath. The fish, in this case, were collected in a trap located at the surface. The results of these two pairs of surveys are tabulated in Tables V and VI. Using the chi-square analysis ($p = 0.10$), the incidences of infection for all parasites, except *Anisakis*

TABLE V. Incidence of the parasites found in *Cymatogaster aggregata*, collected from two British Columbia localities in 1963.

Parasites	Departure Bay (30)[a]	Bowen Island (26)[a]
Nematoda		
Cucullanus sp.	26	0
Anisakis sp. (larva)	0	1
Digenea		
Telolecithus pugetensis	11	3
Copepoda		
Parabomolochus cuneatus	13	0
Ergasilus turgidus	1	10
Haemobaphes diceraus	11	0
Isopoda		
Livoneca californica	8	0
Cestoda		
Eubothrium sp. (larva)	2	0

[a]Total number of hosts examined.

TABLE VI. Incidence of the parasites found in *Cymatogaster aggregata*, collected from two British Columbia localities in 1964.

Parasites	Croyden Bay (25)[a]	Elcho Harbour (25)[a]
Copepoda		
Ergasilus turgidus	17	24
Digenea		
Lecithaster gibbosus	4	1
Neozoogonus californicus	0	20
Monogenea		
Gyrodactylus sp.	17	11
Cestoda		
Eubothrium sp. (larva)	1	0

[a]Total number of hosts examined.

sp. and *Eubothrium* sp., showed significant differences between the populations of *Cymatogaster* at Departure Bay and at Bowen Island. In addition, a difference in the intensity of infection by *T. pugetensis* in the two samples was evident. Of the three hosts from Bowen Island infected with *Telolecithus*, one harboured two specimens of this trematode and the others, one each; in contrast, the 11 infected fish from Departure Bay carried an average of nine flukes per host.

The differences in parasitism in *Cymatogaster* between the Croyden Bay and Elcho Harbour collections are not as distinct as those between the two collection sites (Bowen Island and Departure Bay) of the previous year. However, significant differences are apparent in the incidence of infection by *Ergasilus turgidus* and by *N. californicus* (chi-square with $p = 0.10$). In addition, it should be stated that *Lecithaster gibbosus* was also recovered from a variety of other host species taken in the same collections. This ubiquitous form includes in its range of hosts, fishes as widely divergent phylogenetically as *Gasterosteus aculeatus*, *Clupea pallasi*, *Oncorhynchus* spp., and *Ammodytes hexapterus*.

The British Columbia surveys also offer information which contrasts strongly with that gained from the earlier California collections. A comparison of the parasites of southern populations of *Cymatogaster* with those of northern ones shows that the parasite faunas of this species in these two geographical areas are quite distinct. None of the 59 specimens of *Cymatogaster* which were examined from California harboured any of the parasites which were recovered from the same host species taken in Canadian waters. On the other hand, it is interesting to note that *Telolecithus pugetensis* and *Neozoogonus californicus*, which were quite prevalent in other species of embiotocids in California waters, occur in northern populations of *Cymatogaster*. This distinctness in the parasite faunas is also seen in the other species of parasites which have been recovered in the respective surveys. The three species of copepods are restricted to host specimens taken in the Canadian collections, as were the nematodes, the monogenetic trematode, the parasitic isopod, and the larval cestode *Eubothrium*. An entirely different group of species has been recovered from the California populations of *Cymatogaster*; these parasites included the digenetic trematode *G. acirrus*, a larval Trypanorhyncha, and a juvenile *Corynosoma*.

DISCUSSION

Baer (1952) stated that "host specificity does not necessarily imply that a parasite always occurs in or on one and the same species of host, because it may also occur in or on hosts that are more or less directly related to one another either phylogenetically or ecologically." In addition, it is evident from Rogers (1962) that a number of phenomena observed in the various levels of host–parasite relationships can be explained in purely ecological terms. However, as ably summarized by Rogers, specificity of parasites is dependent on a number of factors, some of which must relate to the physiological depend-

ence of a parasite to a particular host. Manter (1957), when writing of host specificity of Digenea in fishes, stated "the difficulty is to untangle the relationships due to ecological causes and those arising from phylogeny."

Relative to these statements, the results obtained in this study and presented in Table I strongly suggest that phylogeny at the intrafamilial level in the embiotocids cannot be elucidated by use of digenetic trematodes as indices of these relationships. On the other hand, the information given in Tables II–IV suggests that certain Digenea tend to occur in hosts which live in a specific type of environment. The data shown in Tables V and VI are rather conclusive in indicating that the habitats in which *Cymatogaster* exists determines, to a large extent, the parasite fauna which it harbours. This view is further supported by the differences in the parasites harboured by this host species in California and in British Columbia.

ACKNOWLEDGMENTS

I wish to express my appreciation to Drs Gordon H. Ball and Boyd W. Walker, Department of Zoology, University of California, Los Angeles, for their guidance during the earlier phases of this work. I wish to thank various members of the Fisheries Research Board of Canada, more specifically Drs Leo Margolis and Robert Parker of the Biological Station, Nanaimo, B.C., for their invaluable cooperation which was instrumental in the completion of this investigation. In addition, special mention should be made of the financial support extended during the summer of 1963 through Dr Norman Wilimovsky of the Institute of Fisheries, Department of Zoology, University of British Columbia, Vancouver, B.C.

REFERENCES

BAER, J. G. 1947. Les helminthes parasites des Vertébrés. Relations phylogéniques entre leur évolution et celle de leurs hôtes. Conséquences biologiques et medicales. Ann. Soc. Franche-Comté Univ. Besa on, **2**: 99–113.

1951. Ecology of animal parasites. The University of Illinois Press, Urbana. 224 p.

1957. Premier Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés. Paul Attinger, Neuchatel. 324 p.

BAYLIS, H. A. 1938. Helminths and evolution. *In* G. R. de Beer [ed.] Evolution — Essays on aspects of evolutionary biology. Oxford University Press, Oxford, England. p. 249–270.

DOGIEL, V. A. 1964. General parasitology. (English translation of enlarged and revised 3rd edition.) Oliver and Boyd, London. 516 p.

DOUGHERTY, E. C. 1949. The phylogeny of the nematode family Metastrongylidae Leiper, 1909: a correlation of host and symbiote evolution. Parasitology, **39**(3/4): 222–234.

GAMBINO, J. J., AND D. HEYNEMAN. 1960. Specificity and speciation in the genus *Cyrtosomum* (Nematoda: Atractidae). Am. Midland Naturalist, **63**(2): 365–382.

IHERING, H. VON. 1891. On the ancient relations between New Zealand and South America. Trans. Proc. New Zealand Inst., **24**: 431–445.

MANTER, H. W. 1957. *In* J. G. Baer [ed.] Premier Symposium sur la Spécificité Parasitaire des Parasites de Vertébrés. Paul Attinger, Neuchatel. p. 185–196.

METCALF, M. 1929. Parasites and the aid they give in problems of taxonomy, geographical distribution, and paleogeography. Smithsonian Misc. Collections, **81**(8): 1–36.

NOBLE, E. R. 1941. On the distribution relationships between California tide pool fishes and their myxosporidian (Protozoan) parasites. J. Parasitol., **27**(5): 409–415.

1957. Seasonal variations in host-parasite relationships between fish and their protozoa. J. Marine Biol. Assoc. U.K., **36**(1): 143–155.

ROGERS, W. P. 1962. The nature of parasitism. Academic Press, Inc., New York and London.

Electrophoretic Patterns of Blood Serum Proteins from Rainbow Trout (*Salmo gairdneri*)[1,2]

By Robert V. Thurston[3]

Department of Zoology and Entomology
Montana State University, Bozeman, Montana

ABSTRACT

Electrophoretic patterns on acrylamide gels of blood serum proteins from over 400 hatchery rainbow trout (*Salmo gairdneri*) subjected to different environmental stress have been examined. Stresses to which fish were subjected were: reduction of oxygen, addition of copper sulfate, addition of sodium sulfite, and different methods of capture. Comparisons of patterns were made on the basis of sex, degree of maturity, and location of blood extraction. Comparisons were also made with blood protein patterns of wild rainbow trout taken from a local stream.

Patterns showed marked intraspecific differences, and revealed a characteristic band for sexually ripe females. Significant variations were found which were attributed to degree of maturity, method of sampling, repeated sampling of the same individual, and method of capture. No significance was attributed to variations related to reduction of environmental oxygen or the addition of sublethal levels of sodium sulfite. Significant pattern variations were noted with the addition of copper sulfate. Comparisons with wild rainbow trout showed significant pattern differences.

RÉSUMÉ

Des diagrammes électrophorétiques en gel-discontinu de protéines sériques de plus de 400 truites arcs-en-ciel (*Salmo gairdneri*) soumies aux différentes charges d'environnement ont été examinés. Des charges auxquelles des poissons ont été soumies étaient: la réduction d'oxygène, l'addition de sulfate de cuivre, l'addition de sulfite de sodium, et les différentes méthodes d'attrapage. Des comparaisons des diagrammes ont été faites selon le sexe, le degré de maturité, et le point d'extraction du sang. Des comparaisons ont été faites aussi avec truites arcs-en-ciel sauvages prises d'un ruisseau local.

Les diagrammes ont démontré des différences marquées en cette espèce, et ont révélé une bande characteristique pour des femelles sexuellement mûres. Des variations significatives ont été attribuées au degré de maturité, à la méthode d'échantillonnage, au échantillonnage répété du même individu à la méthode d'attrapage. Aucune signification n'a été attribuée ni aux variations ayant rapport à la réduction d'oxygène environnemental ni à l'addition de niveaux sous-létals de sulfite de sodium. Des variations significatives des diagrammes ont été notées avec l'addition de sulfate de cuivre. Des comparaisons aux truites arcs-en-ciel sauvages ont démontré des différences significatives des diagrammes.

INTRODUCTION

Intraspecific differences in the electrophoretic patterns of fish blood serum proteins have been reported by several researchers. Many of these are described in a review by Booke (1964). Changes in the serum protein patterns of fish

[1]Received for publication September 2, 1966.
[2]Contribution from Montana State University Agricultural Experiment Station, Project No. MS-844, Paper No. 776 Journal Series.
[3]Present address: Department of Science, Farmington State College, Farmington, Maine 04938.

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

subjected to lethal concentrations of sodium fluoride were observed by Neuhold and Sigler (1960). Pattern changes related to pollution stress from Kraft pulp mill wastes were reported by Fujiya (1961), and changes as a result of low dissolved oxygen tension and method of capture were studied by Bouck and Ball (1965, 1966). Other electrophoretic studies concerning variations in fish serum proteins were related to: sexual differences and degree of sexual maturity (Rall, et al., 1961; Vanstone and Chung-Wai Ho, 1961; Drilhon and Fine, 1963; Kirsipuu, 1964a; Thomas and McCrimmon, 1964); transferrin polymorphism (Moller and Naevdal, 1966); temperature differences (Meisner and Hickman, 1962); seasonal variations (Saito, 1957; Kirsipuu, 1964b); disease (Sindermann and Mairs, 1958; Fine et al., 1963; Thomas and McCrimmon, 1964); changes in diet (Lysak and Wojik, 1960; Thomas and McCrimmon, 1964). No study was found which included a variety of tests on fish from the same stock.

In the present study electrophoretic patterns of blood serum proteins were determined for 402 hatchery and 12 wild rainbow trout (*Salmo gairdneri*). The objectives were to determine: if a characteristic serum protein pattern is present among fish of the same species and from the same stock; what variations exist among serum patterns of individuals subjected to physical or chemical stress before blood extraction; what variations may exist among serum patterns of hatchery and wild fish of the same species. The study was done between July 1964 and July 1966.

MATERIALS AND METHODS

Test Fish and Holding Facilities

Approximately 450 blood samples were taken from 414 rainbow trout. Of these fish, 402 were from the Bozeman National Fish Hatchery, Montana. These ranged in total length from 15.2 to 34.3 cm and in age from 15 to 25 months. Twelve wild fish of unknown ages from a local stream were used. These varied in total length from 15.2 to 21.6 cm. A total of 340 fish from the same stock was used in tests to compare age and sex differences and effects of physical stress. The remaining 62 fish were from a different stock and were used for chemical stress tests.

The total length, sex, and degree of maturity of each fish were determined after blood sampling. Fish were classified as "immature" if the gonads were poorly developed and if sex was difficult to determine without microscopic examination. Fish were classified as "mature" if the gonads were developed so that sex was apparent without magnification. Mature fish were classified as "ripe" if the gonads were in spawning condition to the degree that eggs or sperm were readily released when the fish were handled.

Outside raceways at the hatchery and laboratory tanks at Montana State University were used for holding test and control fish. The raceways were of concrete (1.8 × 18.5 m), and supplied with spring water having an annual temperature range of 5–15 C. The laboratory tanks were of fiberglass (1.2 m diam), and supplied with dechlorinated city water with a 10–17 C

annual temperature range. The tanks were maintained at 700-liters capacity during all tests. Fish transported to the University from the Hatchery were allowed an adjustment period of 24–48 hr before experiments began. One thousand fish were planted in a local pond which had a surface area of approximately 2500 m^2 and a maximum depth of 7 m. Of these, seven were recovered after 5 days and sampled.

Blood Collection and Preparation

Immediately after removal from their test environments, fish were anaesthetized for a period of 90–120 sec in a solution (0.25 g per liter) of tricaine methane sulfonate (Sandoz M.S.-222). Blood samples were taken by means of a hypodermic syringe. Blood was extracted from the heart by inserting a needle into the center of the isthmus on a line drawn between the origins of the pectoral fins. A No. 18 needle was used which allowed blood to flow freely and with minimum damage to the blood cells. A total of 370 fish was sampled in this manner. In an experiment requiring repeated sampling of the same individual, blood was extracted from the dorsal aorta (Schiffman, 1959) using a No. 22 needle to minimize hemorrhaging and damage to the muscle tissue. A total of 19 fish was sampled by this means. Blood was taken from 25 fish by a variety of other methods, including transversely slitting the isthmus, severing the caudal peduncle, and opening the pericardial cavity to pierce the heart directly. Some satisfactory serum samples were obtained by each of these methods, but none produced clear samples with the consistency of the first two methods described.

Each sample, after being drawn into a syringe, was slowly ejected into a centrifuge tube and stored at 3–5 C for 2–18 hr to allow clotting. Serum was centrifuged at 15,500 $\times$ g for 3–5 min, and stored at −15 C for periods up to 18 months before electrophoresis.

Electrophoresis

The gel electrophoresis method used for serum separation was modified from Davis (1964). An eight-position plexiglass electrophoresis cell was built using platinum electrodes in place of carbon electrodes to eliminate polarization. Double O-rings were used in place of grommets to ensure constant alignment of gel tubes with relation to the poles of the electric field, thereby reducing inconsistencies among tubes and between runs. A separate cell which would accommodate tubes of larger diameter was employed for destaining. The tube diameter difference permitted insertion of stained gels into the destaining tubes without damage. The amount of serum used was usually 1.5 μl, although comparative samples were run in amounts varying from 0.5 to 5.0 μl. The reagent concentrations used for the small pore gel were those recommended by Davis (1964). The large pore gel and spacer gel concentrations were increased by one-third to ensure rapid and firm setting. Freshly purchased acrylamide gave more consistent results than that which had been on hand for over a year without refrigeration. The aniline blue black fixative stain was

re-used no more than once. Both electrophoresis and destaining were performed under refrigeration at 3–5 C to minimize protein denaturation. The electrophoresis was done at 2.5 ma/tube and at approximately 30 v/cm for 1.5 hr. The destaining was accomplished at 5.0 ma/tube and at approximately 20 v/cm for 3–4 hr. Each electrophoresis run included seven test samples and one control sample. The control was horse serum which maintained a constant protein pattern throughout the study.

Data Analyses

Comparisons among gels were made on the basis of protein distribution as reflected in the number of bands, the relative distance migrated, and the concentration. As many as 18 bands were discernable in some gels, although 10 was the maximum number that appeared with consistency. In order to make meaningful comparisons among gels it was necessary to have some common method of comparison. A densitometer tracing or "profile" was obtained for each gel using a National Instruments Laboratory "Chromoscan." A special cam was used in the Chromoscan to approximate a direct relationship between light absorption and protein-bound dye. The height of the profile curve describing any point along the gel was assumed to correspond to the amount of protein-bound dye in the gel at that point. All gel profiles were divided into 10 fractions, corresponding to the 10 most commonly occurring bands.

A representative gel and its corresponding densitometer profile are illustrated in Fig. 1. Although this profile is divided into 10 standard fractions, two bands can be seen grouped in fraction 10, and three bands in fraction 9. The profile indicates the possibility of additional bands in fractions 8 and 6 although these are not clearly discernible in the gel. Fraction 1 contains the most rapidly migrating band and fraction 10 contains the bands with the least electrophoretic mobility. Fraction 10 is directly adjacent to the starting plane for all protein, i.e. the surface between the spacer gel and the small pore gel.

The relative distances these 10 groups of bands migrated from the starting plane were consistent, although there were wide variations in their intensities. These intensity variations occurred among different bands within the same gel and between corresponding bands of different gels. Some of the wide intraspecific variations among rainbow trout serum patterns are illustrated in Fig. 2–5. The patterns obtained from the same serum sample in different gels were consistent, even when run at different times (Fig. 2).

Each pattern profile was measured with a polar planimeter. The area of each profile fraction was computed as a percentage of the whole. Comparisons were then made among profiles on the basis of these percentages for correspondingly numbered fractions. In a test to determine the replicability of this method, two runs were made each containing two gels at four different concentrations of the same serum sample (0.6, 0.9, 1.2, 1.5 μl). At any concentration level the deviation among corresponding protein fractions did not exceed 3% of the total protein.

Statistical comparisons among gel profiles of fish used in a test to determine maturity and sex-related differences were made by a two-way analysis of variance. A one-way analysis of variance and Duncan's New Multiple Range test were used for all other test comparisons. Significance was assigned whenever the probability of random occurrence was less than 5%.

RESULTS

Sex and Maturity

To determine possible pattern variations attributable to sex and maturity differences, an analysis was made of serum samples from 20 male and 28 female rainbow trout which were collected by dip net directly from the hatchery raceway. Two of the males were immature, 14 were mature, and four were ripe. Fourteen of the females were immature, and 14 were mature. The mean values and range for each fraction in each of these sex-maturity categories are presented in Table I.

Significant differences were observed in fractions 6 and 9 which were related to maturity, but none in any fraction which could be attributed to sex. The F values of all fractions are reported in Table II.

Only two ripe females were found in all the hatchery fish tested. Both of these showed amounts of protein in fraction 10 which were too large to measure by the Chromoscan. These bands were estimated to contain more than 70% of the total protein (Fig. 3). Samples from eight mature females observed in other tests also evidenced this exceptional fraction — the gel from one of these is shown in Fig. 3. Fraction 10 did not exceed 13% in samples from males or immature females. An intense band also appeared in serum samples from two ripe rainbow trout and two ripe cutthroat trout (*Salmo clarki*) taken from nearby streams and lakes.

Because of the statistical differences related to maturity, and the observed differences related to sex, certain data were discarded from all subsequent experiments except the experiment concerned with method of capture.

Method of Capture

Comparisons were made among 126 fish to determine the effects of different methods of capture on blood serum patterns. The methods used were: hook and line, gill net, electroshocking, dip net. Twenty-one fish were caught with artificial bait by hook and line after they were placed in an isolated section of the hatchery raceway. Each fish was played for approximately 45 sec, although it was noted that active resistance to capture diminished markedly after 15–25 sec. Eighteen fish were "caught" by a gill net placed in the hatchery raceway. Each fish was placed into the net by hand, ensuring that the threads did not inhibit the opercular apparatus. Fish were left in the net for 4–21 hr before removal for blood extraction. Blood was taken from 39 fish after electroshocking. Twenty fish were electroshocked simultaneously in an isolated raceway section. Five of these were removed, placed in a holding tank, and blood was taken from them within 5 min. The remaining

TABLE I. Serum protein fractions of blood from rainbow trout in relation to sex and maturity. Fractions expressed as per cent of total protein. Number of individuals in parentheses.

Sex and maturity	Fraction No.									
	1	2	3	4	5	6	7	8	9	10
Immature males (2)										
Mean	1.3	28.5	9.8	15.3	5.4	12.5	2.8	4.7	11.5	8.3
Range	0.6–2.0	23.7–33.3	8.8–10.7	11.6–18.9	4.8–5.9	12.0–13.0	2.4–3.2	4.0–5.3	11.2–11.8	7.7–8.8
Mature males (14)										
Mean	1.3	25.2	17.2	13.3	7.5	11.2	2.8	4.5	9.4	7.5
Range	0.8–2.3	15.2–38.2	7.8–32.7	5.7–22.9	3.4–11.6	8.5–16.1	1.3–4.7	2.9–6.3	7.5–11.4	4.9–11.7
Ripe males (4)										
Mean	1.2	21.4	23.1	15.7	4.4	17.2	2.6	3.3	6.6	4.5
Range	0.7–2.0	13.6–31.6	16.2–35.9	11.2–19.5	2.8–5.3	9.0–26.8	2.0–3.0	2.3–4.2	5.5–8.9	4.2–4.9
Immature females (14)										
Mean	1.4	25.6	17.5	12.7	5.1	14.6	3.2	4.3	9.4	6.3
Range	0.5–1.9	13.5–36.8	9.2–33.5	8.3–19.3	2.4–8.8	10.7–19.3	1.8–4.7	2.8–5.8	7.0–11.2	4.3–8.8
Mature females (14)										
Mean	1.6	22.2	20.3	14.3	5.8	10.7	2.5	3.8	8.6	10.1
Range	0.3–2.8	5.0–42.4	6.3–35.4	10.1–18.5	2.2–13.8	4.3–14.6	0.6–6.4	2.6–5.2	4.4–11.8	5.8–33.1

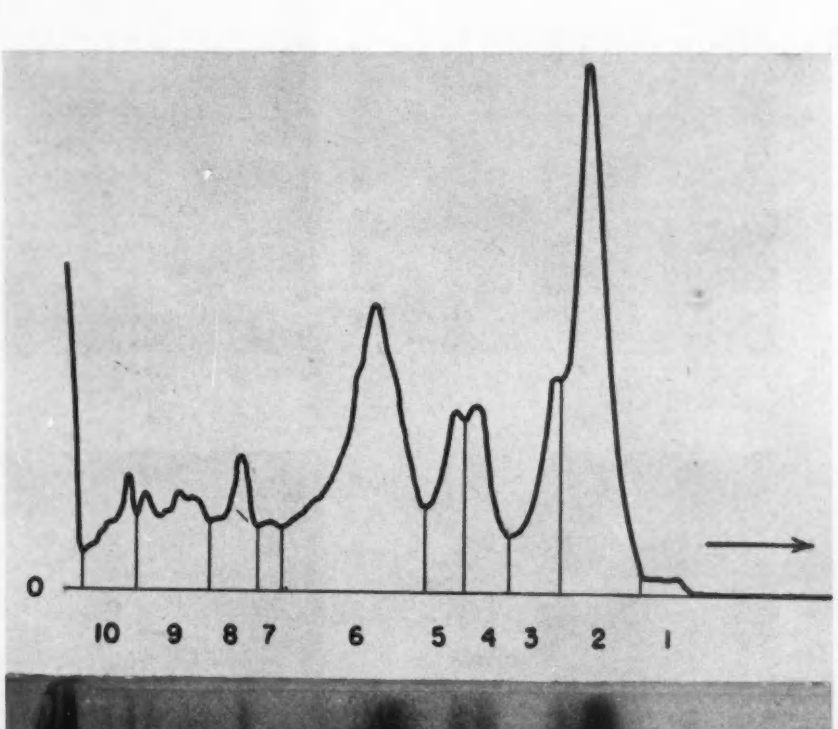

FIG. 1. Disc gel electrophoresis pattern of serum from wild rainbow trout (Fig. 5C) and corresponding densitometer profile. Origin for protein migration is at "0" and direction of migration toward positive electrode is shown by arrow. Numbers indicate profile fractions.

Thurston — J. Fish. Res. Bd. Canada

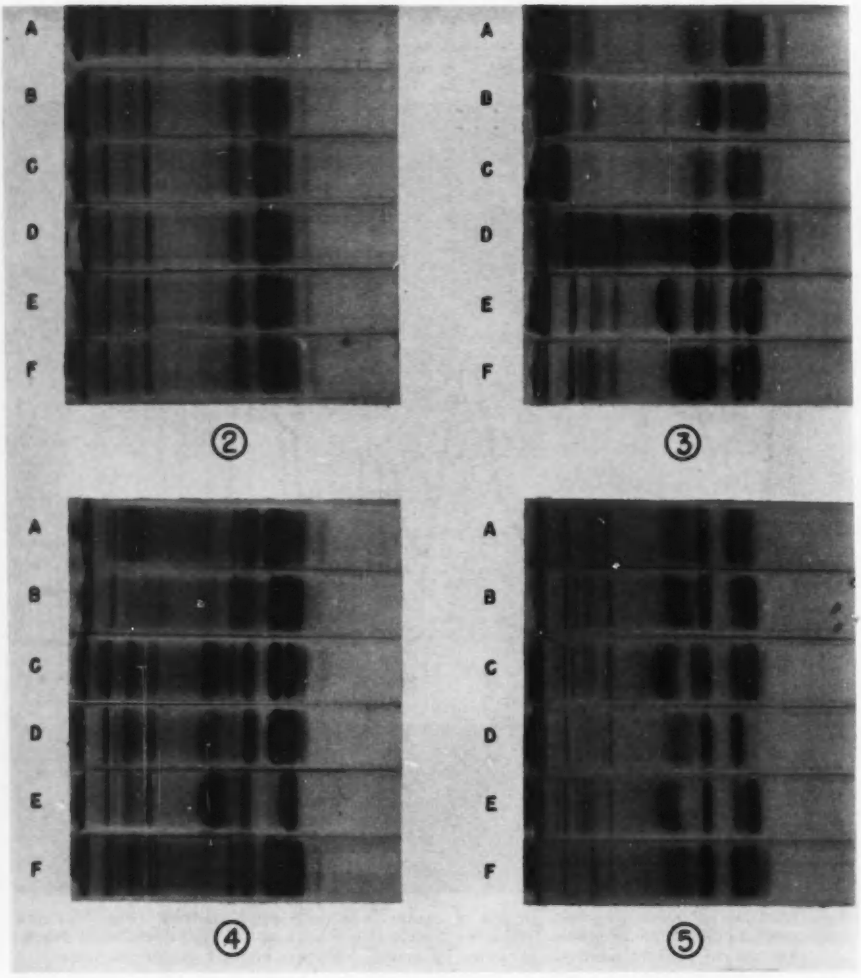

FIG. 2. Patterns from one rainbow trout serum sample: A, B, C run simultaneously, and D, E, F run simultaneously.
FIG. 3. Serum patterns of female rainbow trout: A, B ripe, C, D mature, E, F immature.
FIG. 4. Serum patterns of male rainbow trout: A, B ripe, C, D mature, E, F immature.
FIG. 5. Serum patterns of wild rainbow trout: A, B, D, E mature females, C mature males, F ripe male.

Thurston — J. Fish. Res. Bd. Canada

TABLE II. Profile fraction F values and corresponding significant F values at 95% confidence level.

Experiment	Profile fraction F values										Significant F values
	1	2	3	4	5	6	7	8	9	10	
Sex[a]	1.09	0.15	0.37	0.23	2.93	0.03	0.06	0.85	0.00	0.99	4.08
Maturity[a]	0.39	0.70	1.36	1.04	2.98	9.96[b]	1.16	2.09	6.09[b]	3.04	3.23
Method of capture	7.00[b]	1.86	0.72	3.25[b]	0.96	0.06	0.22	5.12[b]	1.16	3.80[b]	2.68
Repeated sampling (males)	0.21	0.06	0.17	0.12	0.55	0.88	0.69	2.83	2.19	11.03[b]	6.94
Repeated sampling (females)	1.08	0.28	0.29	0.38	0.16	4.53[b]	0.73	0.45	4.03[b]	2.74	3.47
Location of blood extraction	0.83	2.13	0.52	5.69[b]	0.71	0.67	2.36	6.85[b]	1.49	4.88[b]	4.49
Low dissolved oxygen	0.40	4.32	2.71	0.34	2.01	0.13	1.85	1.21	0.02	0.52	4.35
Copper sulfate and sodium sulfite	1.25	0.53	0.02	2.93[b]	0.88	1.43	5.53[b]	1.89	0.72	5.03[b]	2.84
Wild and hatchery stocks	16.64[b]	2.43	0.14	1.26	2.55	69.84[b]	2.24	13.35[b]	0.53	2.70	4.20

[a]Sex and maturity combined in two-way analysis of variance.
[b]Significant differences.

15 fish were then re-shocked, four of these were removed and placed in a holding tank, and these were also sampled within 5 min. This procedure was continued, 4–5 fish being removed after each electroshocking, until the last fish taken from the raceway had been electroshocked five times in a period of 20 min. Another group containing 19 fish was treated in an identical manner. A total of 48 fish was captured by dip net. This was the same group of fish used in the sex and maturity variation study.

Comparisons were made among the serum protein patterns of fish caught by these four methods, and the mean profile values and ranges are presented in Table III. The sex and maturity of these fish are listed in Table IV.

It was not possible to select any one sex-maturity category which contained enough individuals to represent adequately all four capture methods. Accordingly, any interpretation of the data from these experiments must be in the light of possible sex or maturity bias.

The dip net method of capture showed significant differences from all other methods in fraction 1, between hook and line in fractions 4 and 10, and between electroshocking in fraction 8. The electroshocking and hook and line methods showed significant differences between each other in fractions 4 and 8. The two fractions which showed significant differences in sex and maturity experiments showed no significant differences in these experiments.

Repeated Sampling

Four mature males and eight immature females were sampled three times to determine the effect of repeated sampling on blood serum patterns. Each sample contained 0.4–0.6 ml whole blood drawn from the dorsal aorta through the roof of the mouth. During the experiment the fish were held in tanks with a maximum of 15 in each. The second blood sample from each individual was taken 8 days after the first, and the third sample 7 weeks after the second. Blood was taken from additional fish but these sustained considerable tissue damage during one of the first two blood extractions and were removed from the test lot. Some samples were unusable because of excessive hemolysis.

In order to avoid bias in analysis which might result from sex or maturity, the mature males were treated in one group and the immature females in another (Table V). A separate one-way analysis of variance was made on the data from each of these groups. The males showed a significant increase in fraction 10 between the second and third samples, and the females showed a significant increase in fractions 6 and 9 between the first and second samples.

Location of Blood Extraction

An analysis was made comparing the profiles of eight immature females sampled from the dorsal aorta with 10 immature females sampled from the heart to determine possible pattern variations resulting from the location of blood extraction (Table VI). All fish were held in tanks at the University. Data were not analysed for other fish which were bled after severing the caudal peduncle or opening the pericardial cavity because only a few satisfactory samples were obtained from immature females.

TABLE III. Serum protein fractions of blood from rainbow trout captured by different methods. Fractions expressed as per cent of total protein. Number of individuals in parentheses.

Method of capture	Fraction No.									
	1	2	3	4	5	6	7	8	9	10
Dip net (48)										
Mean	1.4	24.3	18.4	13.7	6.0	12.6	2.8	4.1	9.0	7.7
Range	0.3–2.8	5.0–38.2	6.3–35.9	5.7–22.9	2.2–13.8	4.3–26.8	0.6–6.4	2.4–6.3	4.4–11.8	4.2–33.1
Hook and line (21)										
Mean	1.0	28.2	19.4	11.5	6.8	12.3	3.1	4.0	8.2	5.5
Range	0.3–3.0	3.7–49.6	7.9–47.6	7.8–16.1	3.5–16.5	9.8–16.5	1.1–6.1	2.0–6.2	5.9–11.4	2.2–8.5
Gill net (18)										
Mean	0.9	23.3	21.7	13.4	5.7	12.7	3.0	4.5	8.8	6.2
Range	0.3–2.6	4.1–37.9	8.3–50.6	7.8–20.4	4.1–9.5	9.6–18.0	1.8–4.3	2.7–6.9	6.3–11.9	3.6–7.8
Electroshocking (39)										
Mean	0.9	22.5	20.2	14.0	6.2	12.6	3.0	5.0	8.8	6.8
Range	0.3–2.3	4.0–39.6	9.5–35.8	4.8–19.7	2.1–10.6	8.0–23.9	0.8–14.0	3.1–8.2	4.6–11.6	3.4–11.9

TABLE IV. Sex-maturity categories of rainbow trout used in analyses of different capture methods.

Sex-maturity	Dip net	Hook and line	Gill net	Electro-shocking
Immature males	2	6	3	6
Mature males	14	0	0	14
Ripe males	4	4	9	0
Immature females	14	10	6	18
Mature females	14	1	0	1
Ripe females	0	0	0	0
Totals	48	21	18	39

Significant differences in profiles of blood taken from the dorsal aorta and blood taken from the heart were found in fractions 4, 8, and 10.

Low Dissolved Oxygen

An analysis was made of blood serum profiles of 10 fish subjected to low dissolved oxygen for periods up to 48 hr. Duplicate experiments were run in tanks, each involving 10 test and 10 control fish. At the start of each experimental period the incoming water was shut off in both test and control tanks. Dissolved oxygen was maintained in the control tanks by bubbling air through the water, and during the experiments the levels declined from 10.0 ppm to 7.0 ppm. In both test tanks the dissolved oxygen levels dropped from 10.0 ppm to 5.5 ppm during the first 12 hr, to 3.0 ppm after 24 hr, and to 1.3 ppm by the end of 48 hr. In the test tanks the carbon dioxide levels rose from 4.0 ppm to 11.0 ppm, whereas in the control tanks it remained at 4.0 ppm. Ammonia levels in the test tanks rose from 0.5 ppm to 1.8 ppm, and in the control tanks from 0.5 ppm to 1.3 ppm.

Only profiles of immature fish were subjected to data analysis because these comprised the largest maturity group tested. The pooled data (Table VII include four test and five control fish from the first experiment, and six test and seven control fish from the second experiment. No significant differences occurred in the serum fractions between test and control fish.

Copper Sulfate and Sodium Sulfite

The effects of copper sulfate and sodium sulfite on serum protein patterns of 51 fish were studied in a series of four experiments conducted in tanks at the University. Fifteen test and 15 control fish were used in each experiment, although in the final analysis only data from immature fish were used, this being the largest maturity category tested. Incoming water was shut off in both test and control tanks and air was bubbled through the tank water in an attempt to maintain dissolved oxygen levels. Water temperatures rose from 6 to 8 C during the experiments.

TABLE V. Serum protein fractions of blood from rainbow trout subjected to repeated blood extraction. Fractions expressed as per cent of total protein. Number of individuals in parentheses.

Time of sample	Fraction No.									
	1	2	3	4	5	6	7	8	9	10
Males (4)										
First										
Mean	1.0	21.0	18.0	17.1	5.1	11.5	2.8	6.0	9.5	8.2
Range	0.5–1.9	6.3–40.2	5.4–26.7	16.9–18.8	4.4–6.3	9.8–12.7	2.0–3.8	4.4–8.3	8.3–10.6	6.4–9.1
Second										
Mean	1.3	22.4	17.2	16.7	4.8	13.1	2.6	4.4	10.6	7.1
Range	0.6–2.4	14.7–39.2	7.4–26.5	15.3–18.0	2.8–7.0	9.8–15.9	1.2–3.8	3.4–5.3	10.2–11.4	6.1–8.0
Third										
Mean	1.7	24.1	21.3	17.3	4.3	10.9	2.0	4.1	9.2	5.3
Range	0.4–5.4	13.4–42.2	6.0–34.4	15.3–20.1	4.0–4.8	7.5–13.0	1.0–3.2	3.3–5.2	7.7–10.1	5.0–5.7
Females (8)										
First										
Mean	1.3	18.3	26.7	15.1	4.9	11.4	2.0	5.3	8.0	7.1
Range	0.5–2.1	6.6–38.5	7.2–38.5	13.5–18.0	3.3–6.4	9.5–11.8	1.3–2.9	4.5–7.1	6.4–9.9	5.4–8.0
Second										
Mean	1.4	15.6	24.2	15.2	4.8	14.0	2.3	5.0	10.0	7.5
Range	0.5–2.9	4.3–29.5	12.1–33.7	13.2–16.9	3.6–6.3	11.2–18.6	1.7–3.3	3.3–6.3	7.5–11.8	4.1–9.3
Third										
Mean	1.0	15.2	28.0	15.7	4.6	12.7	2.4	5.5	8.9	6.0
Range	0.2–1.7	6.0–26.8	15.6–41.2	13.6–18.7	2.8–5.8	10.6–15.4	1.6–4.0	3.9–7.3	7.7–12.8	4.7–8.9

TABLE VI. Serum protein fractions of blood taken from different locations in rainbow trout. Fractions expressed as per cent of total protein. Number of individuals in parentheses.

Location	Fraction No.									
	1	2	3	4	5	6	7	8	9	10
Heart (10)										
Mean	0.9	25.3	22.8	12.6	5.4	12.3	2.4	3.7	8.8	5.7
Range	0.2–3.3	5.4–35.2	13.5–49.4	9.0–17.5	3.0–7.2	8.6–16.5	1.6–3.0	1.9–7.1	6.3–11.5	3.9–7.8
Dorsal aorta (8)										
Mean	1.3	18.3	26.7	15.1	4.9	11.4	2.0	5.3	8.0	7.1
Range	0.5–2.1	6.6–38.5	7.2–38.5	13.5–18.0	3.3–6.4	9.5–15.3	1.3–2.9	4.5–7.1	6.4–9.9	5.4–8.0

TABLE VII. Serum protein fractions of blood from rainbow trout subjected to low dissolved oxygen, copper sulfate, and sodium sulfite. Fractions expressed as per cent of total protein. Number of individuals in parentheses.

Test	Fraction No.									
	1	2	3	4	5	6	7	8	9	10
Low oxygen (10)										
Mean	1.0	19.1	28.4	11.8	6.4	11.8	2.0	4.6	9.0	6.0
Range	0.3–1.5	4.4–33.6	9.2–41.0	6.4–16.4	3.8–11.2	9.1–19.5	1.2–3.4	2.3–8.1	6.7–12.0	3.7–9.2
Control – Low oxygen (12)										
Mean	1.0	27.4	20.8	12.5	5.2	12.2	2.5	3.9	9.1	5.5
Range	0.2–3.3	5.4–42.0	8.8–49.4	9.0–17.5	3.0–7.2	8.6–16.5	1.5–4.8	1.9–7.1	6.3–12.7	3.6–7.8
Copper sulfate (10)										
Mean	0.8	20.9	14.3	10.7	6.0	21.8	3.1	5.6	9.2	7.6
Range	0.2–1.4	9.9–29.5	5.8–26.4	8.4–12.9	3.5–9.5	16.1–28.2	1.8–4.6	4.0–9.9	5.8–13.0	5.3–12.2
Sodium sulfite-1 (9)										
Mean	0.7	22.3	13.8	10.8	7.6	24.4	2.1	4.2	8.3	5.7
Range	0.3–1.3	15.4–33.6	6.2–20.2	4.3–15.0	2.9–17.3	20.4–28.5	1.1–3.3	2.7–4.9	7.4–11.1	4.8–7.2
Sodium sulfite-2 (12)										
Mean	0.6	18.8	14.2	10.7	7.8	24.4	2.5	4.5	9.4	7.2
Range	0.3–1.2	9.1–31.3	4.4–23.4	6.9–14.5	3.3–13.5	19.6–28.9	1.9–3.2	2.8–6.7	6.5–12.3	5.2–11.8
Control – Copper sulfate, sodium sulfite (20)										
Mean	0.6	20.3	13.8	13.1	6.6	24.1	2.1	5.0	8.6	5.9
Range	0.2–1.2	8.3–33.6	4.8–25.4	6.5–19.9	3.5–15.5	13.4–28.7	1.0–3.4	2.5–8.3	5.0–15.7	3.5–8.0

Sufficient copper sulfate was added to bring the copper ion level to 5.0 ppm in the first copper sulfate experiment. By the end of a 12-hr period all but four fish had died. Blood was then taken from the surviving fish and the experiment was terminated. In the second experiment the copper ion level was also started at 5.0 ppm but it decreased to 1.5 ppm by the end of the test period. Thirteen of the test fish were alive after 9 hr, but experiencing difficulty in maintaining equilibrium. Blood was taken from these fish and the experiment was terminated.

Fish were initially subjected to 400 ppm sulfite ion in the first sodium sulfite experiment. During the first 6 hr they evidenced some difficulty in breathing but after 24 hr their breathing and movement appeared normal. None of the fish died and blood samples were taken from each. The change in dissolved oxygen was from 7.0 ppm to 4.5 ppm during the test period. Starting conditions were identical to the first in the second sodium sulfite experiment, but the experiment was terminated after 2.5 hr. This was the time that fish showed the greatest loss of equilibrium in the first sulfite experiment. Dissolved oxygen dropped from 7.0 ppm to 0.1 ppm in the first 15 min and remained near this low concentration for the rest of the test period.

Because the first copper experiment and its control included only two immature fish, data from this experiment were omitted in the final analysis. The remaining data included 5 males and 5 females from the second copper experiment, 4 males and 5 females from the first sulfite experiment, 5 males and 7 females from the second sulfite experiment, and 9 males and 11 females from the control groups (Table VII). A one-way analysis of variance was made on these three experimental groups and on the combined control groups. The control fish showed significant pattern differences from the copper experimental fish in fractions 7 and 10. The first sulfite experimental fish (those tested for 24 hr) also showed differences from the copper experimental fish in these same fractions. The two sulfite experimental groups showed differences from each other in fraction 10. The analysis of variance also showed significant differences in fraction 4. Differences among groups in this fraction were not revealed by Duncan's New Multiple Range test because the confidence level of 95% significance in the analysis of variance was actually lower than the Range test application level (98% or more).

Large concentrations of sulfite dissolved in water caused a marked decrease in dissolved oxygen. Even so, there were no significant differences between the control fish and either of the groups of fish subjected to sulfite salts. These results are similar to those obtained earlier in the experiment on low oxygen concentrations in which no significant differences were obtained between test and control groups.

Wild and Hatchery Stocks

Nine wild rainbow trout were sampled to see if variations existed between their serum protein patterns (Fig. 5) and patterns of hatchery fish. The wild fish selected were all mature females captured by electroshocking

and transplanted to the University where they were held for an adjustment period of 48 hr before blood sampling. A comparable number of immature females from hatchery stock captured by electroshocking were sampled immediately after capture. Mature hatchery females available for comparison were taken by dip net.

A one-way analysis of variance was made to compare data from serum profiles of wild fish and of both hatchery groups (Table VIII). Significant differences were found between the profiles of wild fish and both hatchery groups in fractions 1 and 6. The hatchery fish which were not electroshocked showed differences from both other groups in fractions 6 and 8. In the experiment on different capture methods a significant difference in fraction 8 was also shown, although none was shown for fraction 6. Differences in fraction 6 between mature and immature fish have also been shown in the experiment on sex and maturity, although none was shown for fraction 8.

DISCUSSION

At the start of the present study both paper electrophoresis and disc-gel electrophoresis techniques were tried. For any one serum sample it was more difficult to replicate the gel pattern than the paper pattern. However, the gel pattern provided a greater number of apparent serum fractions, and because of this it was felt that the potential of the gel for obtaining a more revealing serum profile would be greater. Approximately 15 months of the laboratory phase of this study were spent in developing facility with electrophoretic techniques and in building and modifying electrophoresis separation and destaining equipment. When the degree of replication illustrated by Fig. 2 was achieved, the electrophoretic separation of the serum samples collected in the experiments was begun. As many as 18 fractions were noted in some of these samples and in some as few as 10. Certain gross similarities among these patterns became apparent, and these are characterized by Fig. 3–5. These patterns also have similarities to the disc-gel patterns of rainbow trout plasma reported by Tsuyuki and Roberts (1965, 1966). No two patterns of different serum samples could be considered identical, and few were sufficiently alike that some kind or degree of difference could not be readily perceived. Because of this variety of individual differences, it has not been possible to characterize a "normal" disc-gel electrophoresis pattern for rainbow trout serum.

Changes in the serum profile of any one individual may be brought about by the introduction or increase of a given protein, by the decrease or elimination of a given protein, or by any change in the structure of a protein which is sufficient to alter its electrophoretic mobility. Increased endocrine flow into the blood stream as a result of stress can effect the total serum protein. This change may not be measurable by present methods, although measurable changes in other proteins in response to this flow may occur. Tissue destruction, releasing cellular proteins into the blood stream, may be one of these causes of change in serum protein patterns. The damage may be from trauma

TABLE VIII. Serum protein fractions of blood from wild and hatchery rainbow trout. Fractions expressed as per cent of total protein. Number of individuals in parentheses.

	Fraction No.									
Origin of stock	1	2	3	4	5	6	7	8	9	10
Wild mature females (9) (electroshocked)										
Mean	0.6	13.8	20.0	13.2	3.8	25.6	2.7	6.3	7.9	6.1
Range	0.3–1.1	3.3–30.5	7.8–34.2	8.7–18.1	2.1–5.3	21.9–28.9	2.1–3.4	3.7–9.0	3.4–13.0	4.1–10.2
Hatchery immature females (8) (electroshocked)										
Mean	0.5	19.8	22.0	12.5	5.9	14.0	4.5	6.1	8.9	6.0
Range	0.3–0.7	8.4–28.1	14.1–34.4	7.9–15.6	4.7–8.8	9.1–18.8	1.3–14.0	5.4–8.1	6.5–11.2	4.4–7.7
Hatchery mature females (14) (dip net)										
Mean	1.6	22.2	20.3	14.3	5.8	10.7	2.5	3.8	8.6	10.1
Range	0.3–2.8	5.0–42.4	6.3–35.4	10.1–18.5	2.2–13.8	4.3–14.6	0.6–6.4	2.5–5.2	4.4–11.8	5.4–33.1

or from physiological degradation. Some protein is added to any serum sample as a result of hemolysis during even the most careful blood extraction. Correlations between pattern variations and degrees of hemolysis were not made as part of the present study.

The occurrence of multiple hemoglobins has been reported for several species of fish including rainbow trout (Hashimoto and Matsuura, 1959; Schumann, 1959; Buhler, 1963; Tsuyuki et al., 1965) and rainbow trout hybrids (Tsuyuki and Roberts, 1965). It may be that some of the serum pattern variations reported in the present study are attributable to these cellular polymorphs which enter the serum sample as a result of undetected hemolysis, or under conditions of stress as a result of "cellular leakage" as discussed by Bouck and Ball (1965). Serum transferrin polymorphism has been reported by Moller and Naevdal (1966) who used starch/agar gel electrophoresis and examined the sera of coalfish (*Gadus virens*), pollack (*G. pollachius*), and whiting (*G. merlangus*). Both of these types of genetic polymorphs would be independent of any tests to which fish were subjected, and the possibility of their influence on test data must be recognized.

No reports of intraspecific differences among fish related to repeated sampling of the same individual or to location of blood extraction are known to this investigator, although studies have been made on variations attributable to sex and maturity, method of capture, and chemical stress. Vanstone and Chung-Wai Ho (1961) reported a slowly migrating fraction in the serum of maturing 2.5-year-old female coho salmon (*Oncorhynchus kisutch*) which they believe may be lipovitellin. It was absent from the serum of spawning fish and those that had completed spawning. Rall et al. (1961) described the appearance of a rapidly migrating plasma fraction from mature lampreys (*Petromyzon marinus*), and Thomas and McCrimmon (1964) studied the same species and found serum pattern differences between sexes in the pre-spawning phase which did not appear in the mature phase. Kirispuu (1964a) studied eight Estonian fish and found no intraspecific pattern differences among males and immature females, but albumins and rapidly migrating globulins in mature females increased during the spawning season. Bouck and Ball (1965) used only male fish in their study because of observed sex-related differences. Tsuyuki and Roberts (1966) have noted a fraction separable on acrylamide gel which appears to be similar to the slowly migrating fraction characteristic of ripe females reported in this study (Fig. 3). This fraction has not been identified.

Bouck and Ball (1966) have reported significant differences in plasma protein patterns of rainbow trout caught by seining, hook and line, and electroshocking. They used paper electrophoresis and obtained a profile of five plasma fractions. Comparisons between their patterns and those of the present study are difficult because of the differences in the two separation techniques. However, in each study the pattern differences between any two methods of capture may be the result of different hormonal responses.

Significant differences have also been reported by Bouck and Ball (1965) in the blood plasma profiles of two out of three species of fish studied under

conditions of low oxygen. Changes were noted in two of the six fractions obtained in the paper electrophoresis profiles of bluegills (*Lepomis macrochirus*) and in one of the five profile fractions obtained for largemouth bass (*Micropterus salmoides*). Yellow bullheads (*Ictalurus natalis*) evidenced no profile change, and these authors have suggested that the dissolved oxygen levels (2.7 ppm) in the test conditions may have presented little or no stress for this species. In the present study, no significant changes were noted in the serum profile fractions of rainbow trout subjected to dissolved oxygen levels as low as 1.3 ppm. In addition, no significant changes were noted in the serum patterns of rainbow trout subjected for up to 2 hr to a decrease in oxygen to 0.1 ppm caused by sodium sulfite.

Fujiya (1961) described a protein pattern shift in the blood of *Sparus macrocephalus* exposed to varying concentrations of Kraft pulp mill wastes. He suggested that electrophoretic analysis of fish blood serum might prove to be a useful tool as a pollutant detector. Significant changes were noted in the patterns of rainbow trout subjected to lethal levels of copper sulfate. The full nature of the reactions of copper to fish is not understood. Heavy metals, including copper, are known to form insoluble compounds when combined with proteins in the mucus secreted by the external epithelial tissues of fishes. This condition is known to interfere with respiration (Doudoroff and Katz, 1953; Fromm and Schiffman, 1958). Holland et al. (1960) concluded that blockage by outer epithelial tissue is sufficient to keep heavy metals, including copper, from penetrating to internal tissues. Some recent works show definite histopathologic changes under prolonged conditions of low concentrations of heavy metals (Crandall and Goodnight, 1963) as well as actual tissue accumulation of certain heavy metals (Fromm and Stokes, 1962). If environmental ions deposit in the blood of fish, then it seems possible that pattern changes will occur if these ions combine with serum proteins. Albumins in particular have an affinity for chelating ions, and changes in tertiary and quaternary structures are the immediate result.

In interpreting the results of the tests which revealed pattern differences between hatchery fish and wild fish, consideration must be given to the diet differences of these two groups. Hatchery fish were maintained on meal pellets as opposed to the forage uptake of wild fish. Pattern differences have been reported among the serum samples from carp fed different foods containing varying protein amounts (Lysak and Wojcik, 1960) and also among sea lampreys which had been fasting for different periods of time concurrent to varying spawning stages (Thomas and McCrimmon, 1964).

No observable differences were noted between patterns obtained from the same serum sample when electrophoresed after frozen storage of 2 months and of 7 months. Tsuyuki and Roberts (1966) have reported that prolonged frozen storage of salmon plasma (−30 C up to 12 months) did not affect patterns drastically. Other researchers have stored frozen fish sera at various temperatures, although the time periods were not specified (Sanders, 1964; Thomas and McCrimmon, 1964).

None of the fish used in this study was observed to have any pre-experiment injury, or to be diseased. It does not seem likely that either of these conditions would have caused significant changes in immunoglobulins during any experiment in the study.

CONCLUSIONS

This study revealed considerable variability in the serum protein patterns of rainbow trout from one hatchery stock, and further variability between this stock and a group of wild rainbow trout. In addition to pattern variations among fish not intentionally subjected to conditions of stress, there were also pattern variations among fish subjected to environmental test conditions involving varying kinds and degrees of apparent stress. Significance was attached to these variations. Intraspecific genetically controlled variations may also exist which may add to the complexity of any serum profile. The findings of this study indicate that caution should be exercised in the interpretation placed on electrophoretic patterns in pollution investigations, pathologic examinations, and taxonomic studies.

ACKNOWLEDGMENTS

In am indebted to Dr C. J. D. Brown who directed the study and assisted in the preparation of the manuscript. Thanks are also due to Drs Graeme Baker, Gary A. Strobel, and John C. Wright who gave suggestions during the laboratory work, and to Mr David P. Jacobson who assisted with the data analysis. This investigation was supported in part by United States Public Health Service Research Grants WP 00438 and WP 00125, and Training Grant 5T1-WP-1 from the Division of Water Supply and Pollution Control. Support was also obtained from the Montana Department of Fish and Game, the Montana Department of Health, and the Montana Cooperative Fisheries Unit.

REFERENCES

BOOKE, H. E. 1964. A review of variations found in fish serum proteins. N.Y. Fish Game J., **11**(1): 47–57.

BOUCK, G. R., AND R. C. BALL. 1965. Influence of a diurnal oxygen pulse on fish serum proteins. Trans. Am. Fish. Soc., **94**(4): 363–370.

1966. Influence of capture methods on blood characteristics and mortality in rainbow trout (*Salmo gairdneri*). Ibid., **95**(2): 170–176.

BUHLER, D. R. 1963. Studies on fish hemoglobins. Chinook salmon and rainbow trout. J. Biol. Chem., **238**(5): 1665–1674.

CRANDALL, C. A., AND C. J. GOODNIGHT. 1963. The effects of sub-lethal concentrations of several toxicants to the common guppy, *Lebistes reticulatus*. Trans. Am. Microscop. Soc., **82**(1): 59–73.

DAVIS, J. 1964. Disc electrophoresis – II. Methods and application to human serum proteins. Ann. N.Y. Acad. Sci., **121**(2): 404–427.

DOUDOROFF, P., AND M. KATZ. 1953. Critical review of literature on the toxicity of industrial wastes and their components to fish. II. The metals, as salts. Sewage Ind. Wastes, **25**(7): 802–839.

DRILHON, A., AND J. M. FINE. 1963. Dimorphisme sexuel dans les proteines serique de *Salmo salar*: Etude electrophoretique. Compt. Rend. Soc. Biol., **157**(11): 1897–1900.

FINE, J. M., G. A. BOFFA, AND A. DRILHON. 1963. The proteins of eel serum: Starch gel electrophoresis and immunological studies. Proc. Soc. Exptl. Biol. Med., **114**(3): 651–654.

FROMM, P. O., AND R. H. SCHIFFMAN. 1958. Toxic action of hexavalent chromium on large-mouth bass. J. Wildlife Management, **22**(1): 40–44.

FROMM, P. O., AND R. M. STOKES. 1962. Assimilation and metabolism of chromium by trout. J. Water Pollution Control Federation, **34**(11): 1151–1155.

FUJIYA, M. 1961. Use of electrophoretic serum separation in fish studies. Ibid., **33**(3): 250–257.

HASHIMOTO, K., AND F. MATSUURA. 1959. Multiple hemoglobins in fish. Bull. Japan. Soc. Sci. Fish., **24**(9): 719–723.

HOLLAND, G. A., J. E. LASATER, E. D. NEUMANN, AND W. E. ELDRIDGE. 1960. Toxic effects of organic and inorganic pollutants on young salmon and trout. State Wash. Dept. Fish. Res. Bull. No. 5. p. 223.

KIRSIPUU, A. 1964a. On protein fractions and their sexual differences in blood serum of some food-fishes of the Estonian S.S.R. Eesti NSV Teaduske Akad. Toimetised, Biol. Seeria, **13**(1): 45–54.

1964b. On seasonal changes in blood serum protein fractions of fishes. Ibid., **13**(4): 278–283.

LYSAK, A., AND K. WOJCIK. 1960. Electrophoretic investigations on the blood of carp fed with food containing various protein amounts. Acta Hydrobiol., **2**(1): 49–61.

MEISNER, H. M., AND C. P. HICKMAN, JR. 1962. Effect of temperature and photoperiod on the serum proteins of the rainbow trout, *Salmo gairdneri*. Canadian J. Zool., **40**: 127–130.

MOLLER, D., AND G. NAEVDAL. 1966. Serum transferrins of some gadoid fishes. Nature, **210**: 317–318.

NEUHOLD, J. M., AND W. F. SIGLER. 1960. Effects of sodium fluoride on carp and rainbow trout. Trans. Am. Fish. Soc., **89**: 358–370.

RALL, D. P., P. SCHWAB, AND C. G. ZUBROD. 1961. Alteration of plasma proteins at metamorphosis in the lamprey (*Petromyzon marinus dosatus*). Science, **133**(3448): 279–280.

SAITO, K. 1957. Biochemical studies on the fish blood – X. On the seasonal variation of serum protein components of cultured fish. Bull. Japan. Soc. Sci. Fish., **22**(12): 768–772.

SANDERS, B. G. 1964. Electrophoretic studies of some serum proteins of three trout species and the resulting hybrids within the family Salmonidae. *In* C. A. Leone [ed.] Taxonomic biochemistry and serology. Ronald Press, New York. p. 673–679.

SCHIFFMAN, R. H. 1959. Method for repeated sampling of trout blood. Progressive Fish-Culturist, **21**(4): 151–153.

SCHUMANN, G. O. 1959. An electrophoretic survey of multiple haemoglobins in some freshwater fishes. Rept. Inst. Freshwater Res., Drottningholm, **40**: 176–197.

SINDERMANN, C. J., AND D. F. MAIRS. 1958. Serum protein changes in diseased sea herring. Anat. Record, **131**(3): 599–600.

THOMAS, M. L. H., AND H. R. MCCRIMMON. 1964. Variability in paper electrophoretic patterns of the serum of landlocked sea lamprey, *Petromyzon marinus* Linnaeus. J. Fish. Res. Bd. Canada, **21**(2): 239–246.

TSUYUKI, H., E. ROBERTS, AND W. E. VANSTONE. 1965. Comparative zone electropherograms of muscle myogens and blood hemoglobins of marine and freshwater vertebrates and their application to systematics. Ibid., **22**(1): 203–213.

TSUYUKI, H., AND E. ROBERTS. 1965. Zone electrophoretic comparison of muscle myogens and blood proteins of artificial hybrids of Salmonidae with their parental species. Ibid., **22**(3): 767–773.

1966. Inter-species relationships within the genus *Oncorhynchus* based on biochemical systematics. Ibid., **23**(1): 101–107.

VANSTONE, W. E., AND F. CHUNG-WAI HO. 1961. Plasma proteins of coho salmon, *Oncorhynchus kisutch*, as separated by zone electrophoresis. Ibid., **18**(3): 393–399.

NOTES

Primary Production in Two Small Lakes of the Northern Interior Plateau of British Columbia

The Northern Interior Plateau and Mountains is one of 12 limnological regions in British Columbia as classified by Northcote (1964). This region contains 6568 lakes over 4 ha (10 acres) in area, of which 5856 are less than 101 ha. In early September 1966, primary productivity measurements were made using the C^{14} in situ method in two small lakes of this region during a limnological study of Babine Lake (Narver, 1967). The two lakes were of interest primarily because of proposed research on the growth of transplanted juvenile sockeye salmon (*Oncorhynchus nerka*).

Workburn Lake is located on the Newman Peninsula and Chub Lake is located on the east shore of Babine Lake near Double Island (Fig. 1). Morphometric features of the two lakes are:

Lake	Area (*ha*)	Depth (*m*)		Watershed (*ha*)	Elevation above Babine (*m*)	Distance from Babine (*km*)
		Max.	Mean			
Workburn	48	19	8	180	29	0.8
Chub	69	16.5	7	250	15	0.5

Neither lake has any permanent tributaries and both drain into Babine Lake. The outlet stream of Workburn Lake is precipitous and intermittent but is apparently sometimes passable for adult salmonids. The outlet stream of Chub Lake is also intermittent and is blocked by several major beaver dams, so it is not passable for upstream migrants.

In 1966 Workburn Lake contained natural populations of juvenile coho salmon (*O. kisutch*) and a very few rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*), besides longnose sucker (*Catostomus catostomus*) and lake chub (*Hybopsis plumbea*). There was also a transplanted population of juvenile sockeye salmon. The list may not be complete.

Chub Lake contained at least lake whitefish (*Coregonus clupeaformis*), northern squawfish (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), redside shiner (*Richardsonius balteatus*), longnose sucker, and a cottid.

On September 10, 1966, Chub and Workburn lakes were remarkably similar in the usual indices of productivity (Table I). All of these values were much higher than similar measurements made in adjacent Babine Lake, except that the *p*H was lower (Narver, 1967).

The rates of carbon fixation in these two small lakes can be compared with those of 24 large lakes in western Alaska (Harry et al., 1967); they were

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

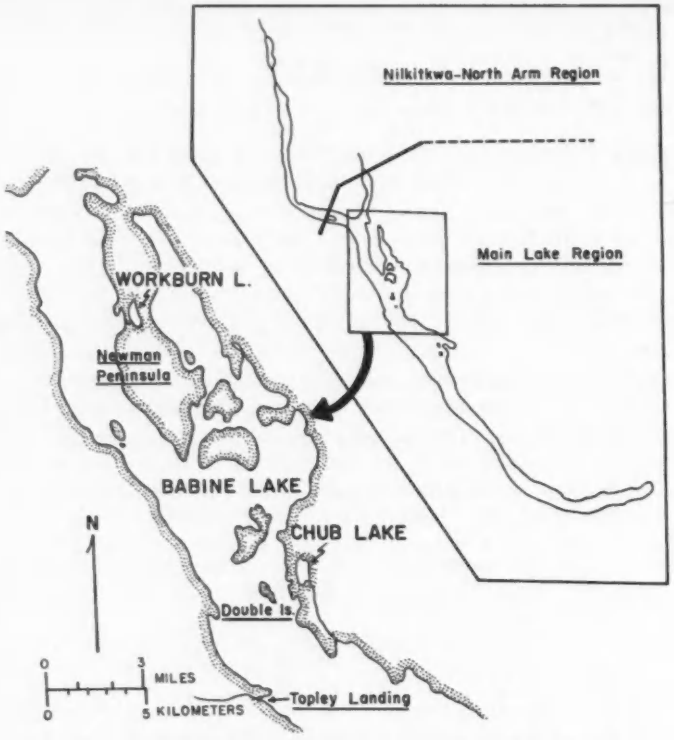

FIG. 1. Workburn and Chub lakes with an inset of Babine Lake.

lower than all but four per unit area but greater than all but four per unit volume of the euphotic zone. These differences are probably partly due to the much shallower euphotic zone in Chub and Workburn lakes; Secchi depth (Table I) was less than those for all but five of the Alaskan lakes. The total alkalinity and available carbon was 2–5 times as great as in the Alaskan lakes.

In both lakes considerable carbon fixation occurred in dark bottles at 13 m (Fig. 2) that may have been the result of bacterial uptake in the oxygen deficient hypolimnion. The *p*H decreased and the alkalinity increased with depth in both lakes:

Lake	Depth (*m*)	Total alkalinity (*ppm* $CaCO_3$)	*p*H
Chub	1	53.30	7.38
	13	60.87	7.22
Workburn	1	56.97	7.60
	13	70.50	6.92

TABLE I. Primary productivity measurements made on September 10, 1966, in Chub and Workburn lakes.

Lake	Time (*hr*)	Radiation[a] (*ly/4 hr*)	Cloud cover	Rate of C fixation/4 hr (mg/m^2)	Rate of C fixation/4 hr (mg/m^3)	pH	T. Alk. (*ppm* $CaCO_3$)	Avail. C (*mg/liter*)	TDS	Secchi depth (*m*)	Compensation depth (*m*)
Workburn	0935	184	1/10	46.867	3.905	7.2	63.73	17.85	108.5	3.5	12
Chub	118	130	1/10	45.056	3.755	7.3	57.09	15.41	106.5	4.5	12

[a]Pyrheliometer located at Topley Landing.

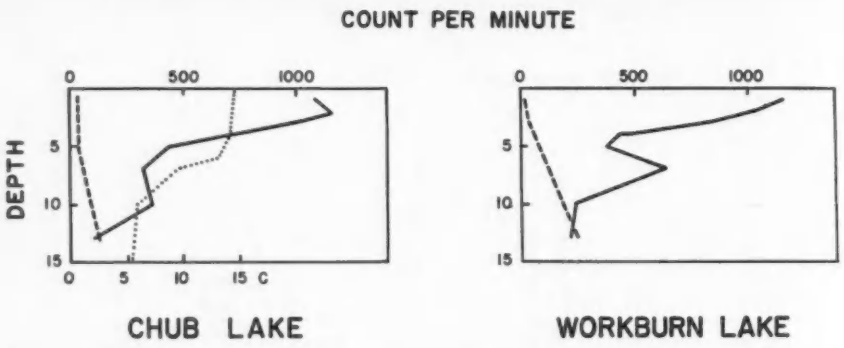

FIG. 2. Beta counts per minute minus background plotted against depth for dark bottle (---) and light bottle (—) in both lakes (September 10, 1966). Temperature profile is included for Chub Lake (...).

These changes suggest anerobic conditions in the hypolimnion.[1] Also, three overnight gill-net sets in Chub Lake caught 269 fish, but no fish were captured at a depth greater than 7 m, which corresponded with the thermocline (Fig. 2).

Growth of the juvenile sockeye in Workburn Lake was far superior to what is typical for Babine Lake. On July 6, 1965, 88,000 fry were released in the lake; this is a density of 183 per hectare. The resulting age I+ smolts in May 1966, averaged 123 mm fork length, compared with the long-term mean length of 81.5 mm for Babine Lake smolts. Perhaps such growth in Workburn Lake was due, in part, to a lack of intraspecific competition. Even disregarding July and August mortalities, the density of fry was somewhat lower than the 1956–63 average August density of 222 per hectare sockeye fingerlings for the main lake region of Babine Lake and it is much lower than the average of 1110 per hectare for the Nilkitkwa–North Arm region (Department of Fisheries of Canada, MS, 1965).

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

DAVID W. NARVER

Received for publication April 17, 1967.

[1]On August 31, 1967 this was confirmed by the following measurements made with Hach Portable Water Analysis Equipment (Model AL-36-WR) in Workburn Lake:

Depth (*m*)	Temp (*C*)	*p*H	Dissolved O_2 (*ppm*)
1	19.0	7.7	10
5	12.2	7.0	4
7	8.5	6.7	0
11	6.0	6.8	0

REFERENCES

DEPARTMENT OF FISHERIES OF CANADA. MS, 1965. Proposed sockeye salmon development program for Babine Lake. Pacific Area, Vancouver. 53 p.

HARRY, G. Y., W. F. ROYCE, C. J. DICONSTANZO, R. L. BURGNER, W. L. HARTMAN, O. A. MATHISEN, AND R. J. ELLIS. 1967. Summary report of studies on the optimum escapement of sockeye salmon in southeastern Alaska, 1961–1962. U.S. Bur. Comm. Fish., Fish. Bull. (In press.)

NARVER, D. W. 1967. Primary productivity in the Babine lake system, British Columbia. J. Fish. Res. Bd. Canada, **24**(10): 2045–2052.

NORTHCOTE, T. G. 1964. An inventory and evaluation of the lakes of British Columbia with special reference to sport fish production. *In* Inventory of the natural resources of British Columbia. B.C. Nat. Resources Conf. p. 575–582.

Pigments from a Sockeye Salmon (*Oncorhynchus nerka*) with Unusual Skin Colouration

On August 20, 1966, a commercially caught, 6-lb, male sockeye salmon (*Oncorhynchus nerka*) was sent frozen to this laboratory with a query as to whether it was "jaundiced." The fish had been taken several days before in the vicinity of the San Juan Islands and was outwardly normal in all respects except for a striking yellow skin colouration which extended dorsally from the tip of the snout to the base of the tail. Internally, the flesh possessed the intense orange–red colour typical of the species and the unusual yellow pigment appeared to be restricted to the skin. In Pacific salmon, flesh colour is due to the carotenoid astaxanthin (Kanemitsu and Aoe, 1958a), and this pigment is very likely also responsible for the red skin pigmentation characteristic of spawning sockeye (Fox, 1957). Since two earlier enquiries had been received about similar freshly caught sockeye and since carotenoid pigments have been reported to be responsible for unusual colours in other marine fish (Bligh and Dyer, 1959), a study of the carotenoid pigments of the specimen appeared desirable.

Pigment analyses, and the gross internal examination (mentioned above), were conducted on the fish which had been stored intact in a polyethylene bag for 2 months at −23 C. Analytical methods were modifications of those employed by Bailey (1937) and Fox (1953).

For analysis, the coloured skin (50 g) was removed, freed of muscle, and finely minced. It was extracted with acetone, followed by successive portions of petroleum ether (PE) (bp 40–60 C) until the extracts were colourless. The pooled extracts were concentrated with a stream of N_2 until approximately 10 ml of a clear amber–yellow oil remained. For comparative purposes, the pigment from muscle was extracted in a similar manner to yield a dark red oil. Pigments were stored at 0 C under N_2.

Samples dissolved in PE were chromatographed on columns of Al_2O_3 (chromatographic grade, McArthur Chemical Co., Montreal, Que.). The Al_2O_3 was first slurried with PE containing 5% (v/v) acetic acid. This released traces of bound CO_2, which otherwise disrupted the columns when fatty acids in the samples (or acetic acid in the eluting fluid) were run through the columns. Before sample application, the columns were washed free of acetic acid with PE. Samples for chromatography, partition tests, or spectral analysis were washed with water and dried with anhydrous Na_2SO_4. Absorption curves were obtained with a Bausch and Lomb Spectronic 505 recording spectrophotometer.

Pigment in Flesh

In the sockeye examined, the characteristic orange–red colour of the flesh was due to a single pigment. After eluting a colourless oil with PE, the

J. Fish. Res. Bd. Canada, 24(10), 1967.
Printed in Canada.

pigment was eluted from the Al_2O_3 column with PE containing 5% (v/v) acetic acid.

In hexane, PE, carbon disulfide, or pyridine, the spectral properties of the native pigment (or its acidic derivative produced during saponification) were typical of astaxanthin (or astacene) isolated from a number of sources (Steven, 1947; Vevers and Millott, 1957; Nishibori, 1959; Tsukuda and Amano, 1966a). More specifically, the sole presence of astaxanthin agrees qualitatively with the muscle pigment studies of Kanemitsu and Aoe (1958a), whose results for Pacific salmon were based on normal fish which had been stored for 3–5 months at –20 C and who, incidentally, considered that the pigment survived storage well enough to justify quantitative pigment determinations on fish held for up to 8 months (Kanemitsu and Aoe, 1958b).

Kanemitsu and Aoe (1958a) considered that the pigment occurred unesterified since it remained in the 90% methanol layer (hypophase) when partitioned with PE. This behaviour was confirmed, but additional tests revealed that unlike free astaxanthin, which is weakly acidic (Goodwin, 1955; Fox, 1960), migration of the pigment into the PE layer (induced by adding water to the system) could not be retarded by the presence of alkali in the hypophase. Esterification with low molecular weight acids (Fox, 1953) best explains the neutral behaviour and partition properties of the muscle astaxanthin.

Pigments in Skin

Skin contained two unidentified, esterified xanthophylls, but no astaxanthin.

Chromatography on Al_2O_3 resolved the skin pigment into two fractions, both of which occurred in the PE layer (epiphase) when partitioned with neutral or alkaline 90% methanol. The major fraction (I) was readily eluted along with the skin oil by PE. The minor fraction (II) was retained as a yellow band but was eluted with PE containing 10% acetone. On drying with N_2, fraction II yielded an orange–yellow waxy material which in hexane exhibited a three-banded absorption curve with a weak inflexion at 418–420 mμ and two stronger bands at 444 and 472 mμ. Fraction I yielded a yellow oil with a similar absorption curve in hexane but with maxima at 420–424 mμ, 450 and 477 mμ. The spectral curves were typical of those of recognized carotenoids (Goodwin, 1955) but differed slightly in specific absorption maxima from any of the listed carotenoids (Fox, 1953; Goodwin, 1955). In addition, after saponification of the skin extract, both pigments became acidic. Dilution of the alkaline hypophase to 25% methanol caused the hypophasic pigments to gather as yellow interfacial flocs which, on acidification, migrated into the PE phase along with fatty acids produced during saponification. In contrast to their neutral precursors, the hydrolysed pigments were tightly retained as a yellow zone on Al_2O_3, where they were bleached before they could be resolved.

In a final experiment on the remaining skin extract, the pigments were removed separately from the diluted, acidified saponification mixture. A major fraction, considered to correspond to fraction I, was obtained which was epiphasic to 75% but not to 90% methanol. The minor fraction (= fraction II) was epiphasic to 25% but not to 65% methanol. Partition behaviour suggested that the pigments were not isomers, but rather two polyhydroxyxanthophylls differing in the number of polar groups present (Fox, 1953; Goodwin, 1955). Unfortunately, during subsequent purification procedures, the minor fraction was again lost. The major xanthophyll was freed of fatty acids (PE elutable) by chromatography on Al_2O_3 and, when eluted rapidly with PE containing 2.5% acetic acid, the pigment was recovered without appreciable loss. Figure 1 compares the spectral curves obtained with the

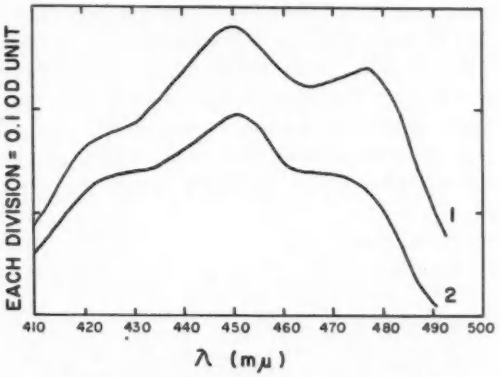

FIG. 1. Characteristic absorption curves of the major skin xanthophyll of sockeye in hexane (1) before and (2) after saponification. Saponification caused similar changes in the form of the spectral curves with other solvents, but in any solvent the λ maximum of the main band remained unchanged: 450 mμ (petroleum ether); 458 mμ (chloroform); and 476 mμ (carbon disulfide).

acidic pigment and its neutral precursor. The acquisition of acidic properties coincided with a change in shape of the absorption curve to a form more typical of the keto-carotenoids (Goodwin, 1955). It is therefore considered that saponification resulted in a keto-hydroxy pigment, possibly related in structure to astaxanthin, or to other acidic carotenoids of uncertain structure (Fox, 1953; Krinsky and Goldsmith, 1960).

Discussion.— The properties of the skin pigments were clearly those of carotenoids. The pigments differed from the yellow, neutral xanthophylls taraxanthin and lutein, which occur as esters in the skins of certain salmonids, and were distinct from astaxanthin, which has been listed as the sole skin pigment of sockeye (Fox, 1957).

Difficulty in identifying the pigments suggested the possibility that the yellow pigments isolated were actually yellow oxidation products derived from astaxanthin during storage (Bligh and Dyer, 1957). This possibility is regarded as remote, however, since some astaxanthin would have been expected to survive (Tsukuda and Amano, 1966b). Also, no traces of pigment other than astaxanthin were found in muscle. It appears more likely that the original pigments were yellow xanthophylls or, at most, that the more highly oxygenated pigment was a storage artifact derived from the original pigment (fraction I).

Mechanisms explaining the existence of the skin colour can only be speculative. Evidence to date suggests that salmonid pigmentation reflects the selective absorption of preformed dietary carotenoids (Fox, 1957; Peterson et al., 1966). This could imply that the sockeye examined differed from the rest of the species in its feeding habits. Physically, there was no obvious reason for a change in diet, and the sole presence of astaxanthin in the muscle is considered to indicate that the fish ingested its normal complement of astaxanthin-rich crustacea (Fox, 1953). Although the unusual pigmentation may have reflected an ability of the specimen to absorb an unusually wide range of ingested pigments, or even the capacity to modify a commonly absorbed pigment, it appears more reasonable to postulate that certain sockeye store large amounts of a pigment which normally occurs at inconspicuous levels.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

T. P. T. EVELYN

Received for publication March 28, 1967.

REFERENCES

BAILEY, B. E. 1937. The pigments of salmon. J. Biol. Bd. Canada, **3**: 469–472.

BLIGH, E. G., AND W. J. DYER. 1957. Yellow discoloration and deterioration in frozen lobster meat. J. Fish. Res. Bd. Canada, **14**: 637–644.
1959. Orange-red flesh in cod and haddock. Ibid., **16**: 449–452.

FOX, D. L. 1953. Animal biochromes and structural colours. Cambridge Univ. Press, Cambridge. 378 p.
1957. The pigments of fishes. *In* M. E. Brown [ed.] The physiology of fishes. Vol. II. Academic Press, Inc., New York. p. 367–385.
1960. Pigments of plant origin in animal phyla. *In* M. B. Allen [ed.] Comparative biochemistry of photoreactive systems. Academic Press, Inc., New York. p. 11–31.

GOODWIN, T. W. 1955. Caretonoids. *In* K. Paech and M. V. Tracey [ed.] Modern methods of plant analysis. Vol. III. Springer-Verlag, Berlin. p. 272–311.

KANEMITSU, T., AND H. AOE. 1958a. Studies on the carotenoids of salmon I. Identification of the muscle pigments. Bull. Japan. Soc. Sci. Fish., **24**: 209–215.
1958b. On the studies of carotenoids of the salmon II. Determination of muscle pigment. Ibid., **24**: 555–558.

KRINSKY, N. I., AND T. H. GOLDSMITH. 1960. The carotenoids of the flagellated alga, *Euglena gracilis*. Arch. Biochem. Biophys., **91**: 271–279.

NISHIBORI, K. 1959. Studies on the pigments of marine animals VII. Carotenoids in the skin and fins of some marine fishes. Publ. Seto Marine Biol. Lab., **VII**: 339–348.

PETERSON, D. H., JAGER, H. K., SAVAGE, G. M., WASHBURN, G. N., AND H. WESTERS. 1966. Natural coloration of trout using xanthophylls. Trans. Am. Fish. Soc., **95**: 408–414.

STEVEN, D. M. 1947. Astacene in the brown trout. Nature, **160**: 507–508.

TSUKUDA, N., AND K. AMANO. 1966a. Studies on the discoloration of red fishes I. Content of carotenoid pigments in eighteen species of red fishes. Bull. Japan. Soc. Sci. Fish., **32**: 334–345.

1966b. Studies on the discoloration of red fishes II. The discoloration of three species during ice and freeze storage. Ibid., **32**: 522–529.

VEVERS, H. G., AND N. MILLOTT. 1957. Carotenoid pigments in the integument of the starfish *Marthasterias glacialis* (L). Proc. Zool. Soc. London, **129**: 75–80.

Line Fishing at Ocean Station P, 50°00′N, 145°00′W

Starting in 1958 the Fisheries Research Board of Canada undertook to provide fishing gear to weatherships' crews operating out of Victoria, B.C. on C.C.G.S. *Stonetown* and *St. Catharines*, in an attempt to augment data from exploratory fishing research vessels. Fishing gear was provided to all crew who would complete a fishing log, showing the hours fished, fishing depth, catch, stomach contents of catch, type of lure, and weather. Scale samples and length and weight of some of the catch were also obtained. Since the arrangement was informal and entirely dependent upon voluntary efforts of the crew, the quality of the reporting and the consistency of fishing was quite variable. However, over an 8-year period, 1958–66, a substantial record of catches has been compiled by a few ardent fishermen.

The gear usually consisted of a hand gurdy with 600 ft (183 m) of sounding wire and a 30-lb (14-kg) weight attached to the end. Secured at 15–30-ft (5–9-m) intervals along the wire were lures on a 6-ft (1.8-m) leader. The lures were commonly available spoons, plugs, feathers, etc., used by commercial fishermen. The method reported here was common to those crew members who consistently caught fish.

Judging from comments in the logs, factors such as weather, ship's speed, time and depth of fishing, persistence and luck, all influence fishing success to some unmeasurable degree. The type of lure, whether commercial or hammered out from a can, was unimportant when fishing was good. Flashers or dodgers on the leader preceding the lure apparently increased the chances of a catch when fishing was poor. There was no record of bait being used in any of the line fishing.

A list of species and numbers caught for the 8-year period are summarized from individuals' logs in Table I. Identifications were made on shipboard by

TABLE I. Fish catch as reported by ships' crews for Ocean Station P, 1958–66.

Common name	Specific name	Number caught
Salmon		841
Promfret	*Brama raii*	2176
Lancetfish (handsaw)	*Alepisaurus borealis*	72
Mackereljack (scad, jack mackerel)	*Trachrus symmetricus*	17
Skilfish	*Erilepis zonifer*	33
Salmon shark (mackerel shark)	*Lamna ditropis*	1
Blue shark	*Prionace glauca*	4
Blue rockfish (priestfish) ?	*Sebastodes mystinus*	1
Frostfish ?	*Benthodesmus simonyi*	1
Squid		1

J. FISH. RES. BD. CANADA, 24(10), 1967.
Printed in Canada.

the crew from illustrations in Clemens and Wilby (1961). All species have been previously reported from British Columbia waters. Two single catch records, *Sebastodes mystinus* and *Benthodesmus simonyi*, are possibly questionable, since they might be confused with more frequently caught species, i.e. *Erilepis zonifer* and *Alepisauraus borealis*. More difficult, even for experienced personnel, is the identification of salmon species when caught in oceanic waters since they look similar. For this reason, the salmon catches were not separated into species but combined as a group. Species identifications in the laboratory based on scale characteristics verified the ships' crews identifications to the extent that 65% of all salmon caught were coho, *Oncorhynchus kisutch*. The large proportion of coho among the salmon caught is of interest, since gillnet and long-line fishing for salmon in the vicinity of Ocean Station P yielded catches predominantly composed of sockeye and pink salmon. Presumably the differences in the species caught is a reflection of selectivity of the fishing methods.

Seasonal changes in relation to catch and effort may best be examined from the logs of crew who fished at every opportunity and recorded both successes and failures. These data were summarized in Table II. The most

TABLE II. Annual catch and effort reported by experienced fishermen, averaged for 1958–66.

Month	Hours fished	Salmon	Pomfret	Mackereljack	Lancetfish
Jan.	70	13			
Feb.	179	60			
Mar.	126	2			1
Apr.	223	26			9
May	206	31			1
June	211	51			1
July	420	15	281	7	1
Aug.	273	0	256	6	6
Sept.	318	1	83	1	1
Oct.	209	0	131	5	1
Nov.	79	3	68		

striking feature is the seasonal composition of the catch. Salmon predominated in catches from January to June, with the largest catches in February and June. Pomfret, the species most frequently caught, were present only in catches from July through December. Similarly, other warmwater species, mackereljack, and blue shark (not shown), were taken only in the latter half of the year. Other species, such as lancetfish and skilfish were taken too infrequently to show a seasonal pattern.

The observation of a seasonal succession of species is supported by findings of Neave and Hanavan (1960) from catches by exploratory fishing vessels in the Gulf of Alaska region. They reported a northward movement of fish

species which conforms to changes in surface temperature. Salmon are replaced, over a wide area of the Gulf, by pomfret, mackereljack, blue shark, and albacore as the surface waters warm. Examination of surface temperature data at Ocean Station P shows that, in years (1960, 1961, and 1963) in which the daily temperatures in June and July increased at an average rate, pomfret were first caught when the surface temperature reached 11.4 C, i.e. in early to mid-July. In other years, notably June 1959 and 1962, when the surface temperature increased rapidly, exceeding the average daily temperature, and then returned to near-average temperatures, pomfret were caught at a lower temperature, 10–11 C, and 2–3 weeks earlier.

A further breakdown of the data is unwarranted since effort cannot be properly measured. For example, the quantity of hooks fished was not recorded and fishing conditions, such as weather and ship's speed, were extremely variable. However, on the basis of remarks recorded in the logs, it would appear that a catch of 1 salmon or 5 pomfret per line per hour was good fishing. The best fishing was in the early morning with vessel drifting at 1–2 knots. Only skilfish were reported as being schooled although salmon and particularly pomfret must have been very numerous at times. On the one occasion when skilfish were reported schooled, 29 of the 33 skilfish were caught.

Both salmon and pomfret showed increases in weight during their respective periods of availability. Salmon increased from 1 to 2 lb (.45–.9 kg) in February to 4–5 lb (1.8–2.3 kg) in June. Pomfret weighed 1–3 lb (.45–1.4 kg) in July and 2–4 lb (.9–1.8 kg) in November. The lancetfish ranged from 2 to 40 lb (.9–18 kg) while skilfish were all small weighing under 2 lb (.9 kg).

Examination of the stomachs showed that two-thirds of the fish had empty stomachs and the remainder contained squid. All the line-caught fish apparently were utilizing the same food base, i.e. squid. Occasionally, a stomach also contained small fish or shrimp, but none of the species, other than skilfish, were reported with zooplankton among the stomach contents.

It is a pleasure to acknowledge the efforts and enthusiasm of the crews of C.C.G.S. *Stonetown* and *St. Catharines*, in particular that of Messrs Bruce Middler, Werner Franke, and Harold Watkins. Without Mr Watkins' enthusiastic support, persistence, and good fishing, the program might never have been undertaken on a continuing basis.

Fisheries Research Board of Canada, R. J. LeBrasseur
Pacific Oceanographic Group, Nanaimo, B.C.

Received for publication April 25, 1967.

REFERENCES

Clemens, W. A., and G. V. Wilby. 1961. Fishes of the Pacific coast of Canada. 2nd ed. Bull. Fish. Res. Bd. Canada, No. 68. 443 p.

Neave, F., and M. G. Hanavan. 1960. Seasonal distribution of some epipelagic fishes in the Gulf of Alaska region. J. Fish. Res. Bd. Canada, 17(2): 221–233.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

1157. WERNER, A. E. 1965. An apparatus for studying hydrogen sulfide oxidation kinetics. Canadian J. Chem., **43**: 3096–3099.

1158. DICKIE, L. M., AND J. E. PALOHEIMO. 1965. Heterogeneity among samples of the length and age compositions of commercial groundfish landings. Intern. Comm. Northwest Atlantic Fish. Res. Bull. No. 2. p. 48–52.

*1159. ACKMAN, R. G., C. S. TOCHER, AND J. MCLACHLAN. 1966. Dimethyl-β-propiothetin: Determination by reactor gas–liquid chromatography, occurrence in algae, and implications in fisheries. Proc. Fifth Intern. Seaweed Symp. 1965. p. 235–242.

1160. DICKIE, L. M. 1965. Difficulties in interpreting trends in cod and haddock landings from the eastern Scotian Shelf. Intern. Comm. Northwest Atlantic Fish. Res. Bull. No. 2. p. 80–82.

1161. DOMBROWSKI, HEINZ, CARLO G. I. FRIEDLAENDER, ROBERT KÜHN, AND DOUGLAS H. LORING. 1965. Bacteriological investigation of carboniferous rock salt from Pugwash, Nova Scotia. Eclogae Geol. Helv., **58**(2): 967–974.

1162. PLATFORD, R. F., AND THOMAS DAFOE. 1965. The activity coefficient of sodium sulfate in seawater. J. Marine Res., **23**(2): 63–68.

1163. ACKMAN, R. G. 1967. Calculation of ECL values in the gas–liquid chromatography of multiple-branched fatty acids. J. Chromatog., **28**: 225–231.

1164. CLEUGH, T. R. 1966. *Caligus vicarius* Hewitt, 1963 (Caligidae: Copepoda), an invalid name. Canadian J. Zool., **44**: 771–772.

1165. BELL, GORDON R. 1966. On the microbial flora of stream-incubated eggs of the Pacific salmon (*Oncorhynchus*). Bull. Office Intern. Epizooties, **65**(5-6): 769–776.

*1166. GROOT, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour, Suppl. XIV. 198 p.

1167. IDLER, D. R., AND B. TRUSCOTT. 1966. The biosynthesis of 1α-hydroxycorticosterone by cartilaginous fish (*Raja*). Excerpta Med. Intern. Congr. Ser. No. 132. Proc. Second Intern. Congr. Hormonal Steroids. p. 1041–1046.

1168. IDLER, D. R., AND B. TRUSCOTT. 1967. 1α-Hydroxycorticosterone: Synthesis in vitro and properties of an interrenal steroid in the blood of cartilaginous fish (Genus *Raja*). Steroids, **5**: 457–477.

1169. THOMAS, M. L. H. 1967. *Thracia conradi* in Malpeque Bay, Prince Edward Island. Nautilus, **80**(3): 84–87.

1170. BROCKERHOFF, H. 1967. Stereospecific analysis of triglycerides: an alternative method. J. Lipid Res., **8**: 167–169.

1171. ANTIA, N. J., AND V. CHORNEY. 1967. Nature of the aldolase activity in a unicellular red alga. Nature, **214**(5092): 1028–1029.

1172. PARSONS, T. R., R. J. LEBRASSEUR, AND J. D. FULTON. 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J. Oceanog. Soc. Japan, **23**(1): 10–17.

1173. MOUNIB, M. S. 1967. Metabolism of pyruvate in testes of fish and rabbits with particular reference to *p*-nitrophenol and 2,4-dinitrophenol. Comp. Biochem. Physiol., **22**: 539–548.

1174. MOUNIB, M. S. 1967. Metabolism of pyruvate by the ovarian tissue of cod. Exptl. Cell Res., **46**: 610–612.

1175. ACKMAN, R. G. 1967. The influence of lipids on fish quality. J. Food Technol., **2**: 169–181.

1176. BOURNE, NEIL. 1966. Relative fishing efficiency and selection of three types of scallop drugs. Intern. Comm. Northwest Atlantic Fish. Res. Bull. No. 3. p. 15–25.

1177. ACKMAN, R. G., J. C. SIPOS, AND P. M. JANGAARD. 1967. A quantitation problem in the open tubular gas chromatography of fatty acid esters from cod liver lipids. Lipids, **2**(3): 251–257.

Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies," composed of two parts. These are distributed to a selected mailing list. (Articles numbered 1020 to 1109 appeared in the Studies for 1966, Part 2).

*Indicates a "Titles only" paper which will not be included in the binding.